

THE IMPACT OF WET SEASON AND DRY SEASON PRESCRIBED FIRES  
ON MIAMI ROCK RIDGE PINELAND, SOUTH FLORIDA

BY

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In the subtropical pine forests on oolitic limestone in Dade County, Florida, Pinus elliottii var. lensa grows over a species-rich understory (> 128 spp.) of shrubby hardwoods (mostly tropical evergreen species), palms, and herbs, including several endemic taxa. Fires prevent rapid conversion to hardwood forest. To compare the response of these pinelands to burning during the lightning fire season (hot, wet, summer months) and the management fire season (cooler, drier, winter months), paired burns were conducted at two sites in Everglades National Park, one burned 3.5 yr previously and the other 6 yr. Aboveground understory

biomass and nutrients were measured immediately before and after, and at 2, 7, and 12 mo after the four burns.

The burns topkilled all the understory vegetation. The fires volatilized 1-1.5 kg/m<sup>2</sup> of organic matter and 5.7-9.5 g/m<sup>2</sup> of N. Meteorological inputs and symbiotic and nonsymbiotic fixation should easily replace N lost in the burns. Losses of P, K, Ca, and Mg were not detectable except for K in one of the burns.

The rapid understory recovery was almost entirely vegetative regrowth of the topkilled plants. Pine seedlings were abundant after the wet season burns, however. Herbs and palms recovered dry mass more rapidly than hardwoods and reached preburn levels within 1 yr. Hardwoods recovered only 18-39% of their preburn biomass. Total understory vegetation recovery was 27-63% of initial amounts, but leaves recovered 58-93%. Net primary productivity the first year after burning was 144-200 g/m<sup>2</sup>.

Recovery of nutrients was more rapid than biomass because of higher nutrient concentrations in regrowth tissues. Some herb and palm nutrient standing crops reached preburn levels within 2 mo.

After the burns litter mass and nutrients often showed an initial decrease before recovery began. At 1 yr litter mass was 42-62% of the preburn amount. Annual pine needlefall averaged 260 and 320 g/m<sup>2</sup> at the two sites.

The amount of hardwood recovery was not determined by season of burning; higher fire temperatures (wet season burn in one case, dry season burn in the other) resulted in less recovery.

## CHAPTER I INTRODUCTION

The importance of fire as an environmental factor influencing ecosystem structure and function is widely appreciated today (Ahlgren and Ahlgren 1960, Kozlowski and Ahlgren 1974, Mooney et al. 1981, Rundel 1981, Wright and Bailey 1982). Fire is often thought of as a succession-initiating disturbance (White 1979). However, in communities that have evolved under a regime of frequent fires, it is the exclusion of fire that may result in dramatic--if not sudden--changes. Much of southeastern U.S., particularly the coastal plain, is covered with vegetation that requires periodic burning (Christensen 1981). Many southern pine forests, for example, develop into hardwood forests in the absence of burning (Garren 1943).

The regrowth vegetation in some frequently burned ecosystems comes from seeds present in the soil or released from killed plants. More commonly, however, individuals survive and sprout back from belowground parts. In chaparral it is common for species to show mixed seedling and sprouting recovery mechanisms (Keeley and Keeley 1981).

Fire is very prominent in South Florida ecosystems, both in terms of area burned and is a determinant of vegetation pattern (Robertson 1953, Wade et al. 1980). Of particular interest in this study are the subtropical pinelands found on the Miami Rock Ridge in southeastern Florida. These pine forests differ from other southeastern coastal plain pine forests in two ways: they include a large number of tropical species in the understory and they grow directly on a limestone substrate nearly devoid of soil.

Prescribed fire is used throughout the southern pine region for site preparation, fuel reduction, and range improvement. It has also become a tool in natural area management in places such as Everglades National Park. In most southeastern pine forest types (with one major exception) fire does not kill the canopy trees as it does in many coniferous forests (Hinselman 1973). This, along with its common use for other purposes, may be why the use of intentionally set fires was so readily accepted as a management technique in natural areas.

Prescribed burns in the southeast are traditionally carried out during the cooler months because fires during this time are less likely to damage overstory trees and because the resprouting vegetation provides forage which is otherwise limited at this time. Before the influence of humans, however, fires were primarily ignited by lightning, which occurs during warmer months.

### Objectives

I wished to examine some ecosystem-level responses of Miami Rock Ridge pinelands to fires during the natural lightning-caused fire season and the traditional management fire season. I was particularly interested in the following:

- (1) The amount of mineralization and loss of organic matter and nutrients due to fires.
- (2) The pattern of recovery of understory mass and nutrients during the first year after burning.
- (3) The degree of recovery of the understory 1 yr after burning, with emphasis on the recovery of hardwoods.
- (4) Based on the above items, to draw some conclusions about the potential role of fire in nutrient cycling and the use of prescribed fire in the management of a natural area.

### The Ecosystem

#### Climate

The climate of South Florida has two salient features: (1) moderate, almost frost-free winter temperatures and (2) a marked seasonality in rainfall (Fig. 1). These characteristics result in a hot period of high rainfall (May-Oct.) and a cooler period of much lower precipitation (Nov.-April). These are known as the wet and dry seasons, respectively, in keeping with tropical terminology.

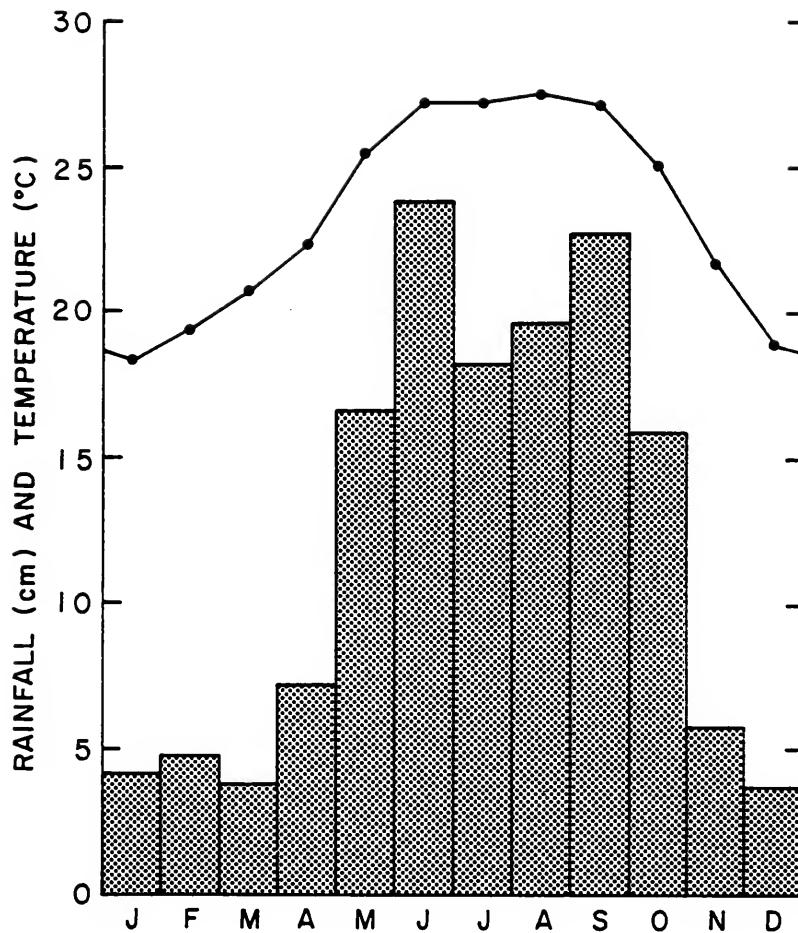


Figure 1. Mean monthly precipitation (bars) and temperature (dots) at Royal Palm Ranger Station, Everglades National Park (after Rose et al. 1981). Mean annual rainfall is 146.3 cm.

Mean monthly temperatures range from about 18.5°C in December and January to about 27.5°C in July and August. Frosts occur in the Homestead area about once every two years on the average (Bradley 1975). These frosts can damage winter vegetable crops and production of avocados and mangos for the ensuing year. Many of the native plant species are also susceptible to frost damage (Craighead 1971), especially plants in open areas. Freezing temperatures were recorded during both 1981 and 1982, but the study areas were little affected. Only a few of the minor species dropped leaves and none had stems killed.

Total annual rainfall averages 146 cm in the southern portion of the Miami Rock Ridge, with almost 90% (117 cm) coming during the six wet season months (Fig. 1). Water levels vary seasonally with a maximum in September and a minimum in April. During the wet season clouds build up in the afternoon and result in brief thundershowers; the lightning that accompanies these storms is a potential ignition source for wildfires. Although most summer rainfall is convectional, tropical cyclones can bring large amounts of rain. In August 1981 Long Pine Key in Everglades National Park received more than 40 cm of rain in three days from tropical storm Dennis.

The southeastern coastal area of Florida can expect a tropical cyclone once every 5 yr and a hurricane-force storm once every 7-8 yr (Gentry 1974). The damage to vegetation

in South Florida by hurricane Donna in 1960 was substantial, especially in the mangroves on the southwest coast (Craighead and Gilbert 1962). The pinelands of Everglades National Park suffered little damage in spite of experiencing wind speeds greater than 160 km/hr. The high water levels brought on by heavy precipitation can affect the pineland vegetation more strongly than the high winds.

Although South Florida is north of the Tropic of Cancer (Long Pine Key is about 25° 23' N latitude) it is commonly referred to as "tropical Florida," especially by those concerned with floristics (e.g., Tomlinson 1980, Long and Lakela 1971). In fact, a world-wide climatic classification scheme based on that of Koeppen (Critchfield 1974) considers the southern tip of Florida to have an Aw, or tropical savanna, climate of the wet-and-dry tropics. It is included as a tropical climate only because the mean monthly temperature of the coolest month is greater than 18°C. The common occurrence of frost at sea level would perhaps make subtropical a better designation for the climate. The classification system of Holdridge (1947), which is based on temperature and precipitation, places southern Florida in the Subtropical Moist Forest life zone.

### Geology and Soils

South Florida is extremely flat: a function of its marine depositional history, low elevation, and relatively short period of emergence. The broad, shallow Everglades basin which extends south from Lake Okeechobee is bounded on the east by the slightly higher Atlantic coastal ridge. The southern end of this ridge in Dade County is an outcropping of oolitic limestone known as the Miami Rock Ridge (Davis 1943). This region, previously dominated by pine forests, extends from the vicinity of Miami southwestward to Homestead and westward into Everglades National Park (Fig. 2). The maximum elevation of the ridge is about 7 m in Coconut Grove (Hoffmeister et al. 1967) and it drops to less than 2 m in Everglades National Park, where it disappears under the surrounding wetlands.

The Miami Limestone (Hoffmeister et al. 1967) which makes up the Miami Rock Ridge is the surface rock of virtually all of Dade County. It represents Pleistocene marine deposition of calcium carbonate during the Sangamon stage (Cooke 1945). The upper oolitic facies which forms the rock ridge is composed of ooids, pellets, and some skeletal sand. To the north along the coastal ridge the limestone is blanketed by a layer of Tamlico sand, and at lower elevations to the west and south it may be covered with late Pleistocene or Recent marls and peats. Several transverse depressions passing through the ridge represent valleys in the rock that have

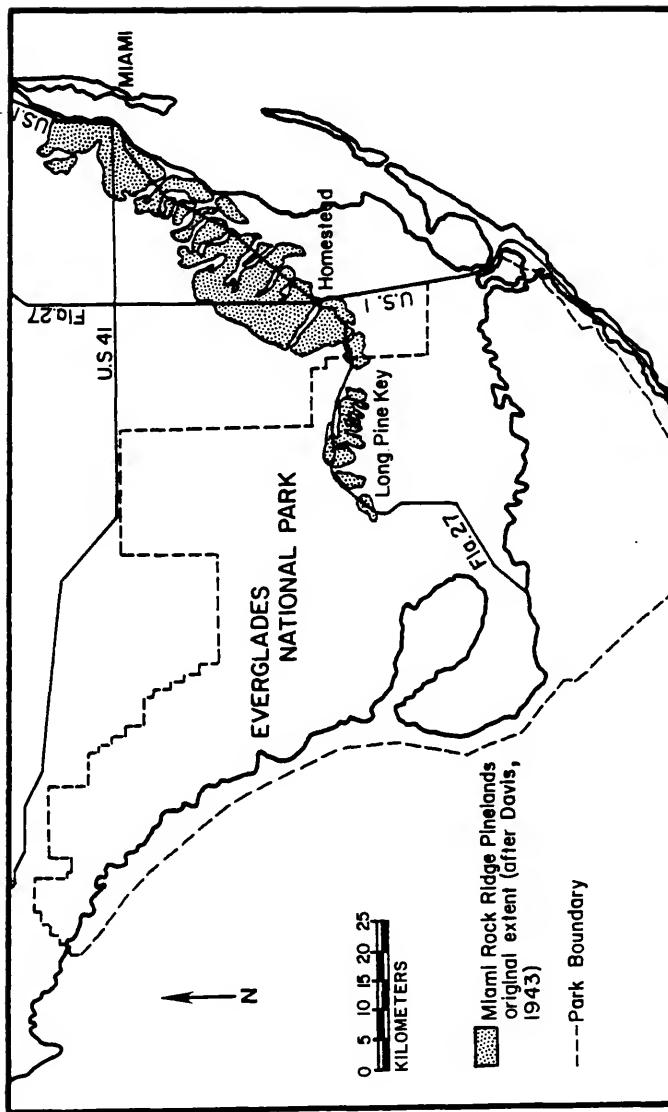


Figure 2. Original distribution of the Miami Rock Ridge pinelands (after Davis 1943).

been partially filled by deposition of marl and/or organic matter (Figs. 2 and 4).

The formation of the Miami Rock Ridge is described by Hoffmeister et al., (1967). They compare it to processes occurring today on the northwest section of the Great Bahama Bank, where loose mounds of ooids are forming and shifting in the shallow water on the eastern edge of the Straits of Florida. The tidal channels that cut through the broad ridge of unconsolidated oolitic sediment are thought to be analogous to those that form the transverse valleys in the Miami Rock Ridge.

The oolite rock is soft and friable until indurated by exposure to the atmosphere. Dissolution of the rock has left the surface honeycombed with numerous holes and fissures, and armed with sharp, jagged projections. In its most treacherous form it is known as pinnacle rock. The diameter of solution holes can range from centimeters to meters as can the depth, although 0.5 m diameter and 1 m depth might be common dimensions for the larger holes. The character of the rock surface varies from place to place, with differences in the degree of solution and the amount of loose rock fragments on the surface.

In the pineland areas of the Miami Rock Ridge the scanty soil is found in solution holes, depressions, and cracks in the rock. The soils are members of the Rockdale series, which is classified as a Lithic Ruptic-Alfic Eutrochrept,

clayey, mixed, hyperthermic (Soil Survey Staff 1975). The surface soils range from dark grayish brown to brown fine sands or fine sandy loams. The subsurface layers (where present) are light gray to yellowish-red fine sand and brown to reddish-brown sandy or clay loams (Soil Conservation Service 1958). In the northern portions of the ridge in the Miami area, the soils tend to be very sandy due to deposition of sands during the Pamlico stage. To the south there are often reddish-brown residual soils; the predominance of these soils in the area just north of Homestead is responsible for the appellation "Peatlands" given to the area. In most areas there is little soil exposed on the surface and plant roots run through cracks and channels in the rock that are filled with a mixture of organic matter and weathering products of the limestone. Because the rock ridge is the highest part of the landscape and is formed of porous limestone the soils are generally well-drained. However, high water tables can reach the ground surface in the lower lying areas during the wet season. The soils are neutral or slightly alkaline in reaction and are deficient in N, P, and K for agricultural crops. The fact that the exploitable soil volume is so small also contributes to making this a very oligotrophic ecosystem.

The nearly frost-free dry season makes southern Florida an important production area for winter vegetables. Current farming practices require extensive site preparation before

production. After bulldozing off the native vegetation the surface 15 cm of rock is scarified with heavy equipment (rock plowed), resulting in a "soil" composed of a mixture of rock fragments, pulverized limestone, and a small amount of original soil. This treatment increases the rooting volume and raises the pH to 8 or higher. Crops (such as tomatoes, squash, and pole beans) require heavy fertilization and irrigation. Experience in Everglades National Park suggests that once the substrate has been altered in this way the native vegetation does not normally reestablish.

#### Vegetation

The vegetation of the Miami Rock Ridge is essentially a mosaic of three basic vegetation types: pineland, hammock, and prairie. The pinelands form the dominant matrix on the higher ground, with small islands of tropical hardwood forest known as hammocks scattered within this matrix. In the shallow transverse depressions that run through the ridge are herbaceous prairies, or glades, similar to the vegetation bordering the ridge. Long (1974) estimates that the vegetation of South Florida is about 5,000 yr old. General descriptions of the natural vegetation of southern Florida, including the rock ridge, have been provided by several authors: Harshberger (1914), Harper (1927), Davis (1943), Craighead (1971), and Wade et al. (1990).

Hammocks are patches of closed forest of essentially evergreen, broadleafed trees. They are found in the higher areas of the ridge where they are seldom flooded, if ever. The soil is a thick layer of organic matter that has accumulated on the surface of the limestone. Important canopy species include Nectandra coriacea, Coccoloba diversifolia, Quercus virginiana, Lysiloma latisiliquum, Metopium toxiferum, Ficus aurea, Bumelia salicifolia, and Bursera simaruba (Phillips 1940, Alexander 1967, Craighead 1974, Olmsted et al. 1980a). Of these only Q. virginiana is not a typically tropical species. The understory consists of saplings of the canopy species, a number of small tree species, and a few shrubs. Relatively few herbs are present on the ground, but epiphytic bromeliads and orchids are quite common.

The seasonally flooded prairies that border the lower fringes of the pineland are dominated by grasses and sedges (e.g. Muhlenbergia filipes and Cladium jamaicense) but include numerous forbs (Porter 1967, Olmsted et al. 1983). Here the water table is above the ground surface for 2-4 mo/yr and the limestone is topped with a thin layer of marl (Olmsted et al. 1980b).

The pinelands, which occupy most of the Miami Rock Ridge, are monospecific stands of Pinus elliottii var. densa, the South Florida slash pine, with a diverse understory of palms, hardwoods, and herbs. The South Florida variety of

slash pine differs from the commercially important northern variety (*var. elliottii*) in several respects (Little and Dorman 1954a,b). Most conspicuous is the grass-like seedling stage reminiscent of *Pinus palustris* (longleaf pine) in which the seedling grows for several years without stem elongation. However, Squillace (1965) showed more or less continuous variation across the range of slash pine for 12 traits, including seedling height and stem diameter. The range of South Florida slash pine extends from the Lower Florida Keys to about Polk County in the center of peninsular Florida and Levy and Volusia Counties along the Gulf and Atlantic coasts, respectively (Langdon 1963). Sandy flatwoods are a more widespread habitat for South Florida slash pine than the limestone of the Miami Rock Ridge.

In contrast to the monotony of the pine overstory, the understory is relatively species-rich. The shrub layer is composed of 15-25 hardwood species per 0.16 ha (Loope et al. 1979), most of which are tree species maintained as shrubs by repeated fires; the palms *Sabal palmetto*, *Serenoa repens*, and *Coccothrinax argentata*; and a cycad, *Zamia pumila*. Hardwoods commonly found as shrubs in the pinelands and as trees in hammocks include *Metopium toxiferum*, *Eumelia salicifolia*, *Mycrsime floridana*, *Guettarda scabra*, and *Ardisia escallonioides*. Most hammock tree species are found at least occasionally growing in pineland. Some smaller

shrubs (e.g. Dolomedea viscosa, Lantana depressa, and L. involucrata) are found in the open pinelands but not in the shade of hammocks.

Most of the hardwoods are West Indian in distribution and are found only in extreme southern Florida or along the coast to northern Florida. Only a few of the more important species are found as far north as Gainesville, Florida: Rhus copallina, Myrica cerifera, Ilex cassine, Persea borbonia, and Quercus virginiana. Notably absent from the rock ridge pinelands are Ilex glabra (gallberry) and members of the Ericaceae, so important in most southeastern pinelands. Apparently the high soil pH excludes these species. The biogeography of pineland shrubs in South Florida, including the Miami Rock Ridge, has been detailed by Robertson in Olmsted et al. (1983).

The herb layer is dominated by grasses but also contains sedges, forbs, and three common ferns. The number of herb species per 0.16 ha varies from 50 to 75 (Loope et al. 1979). The relative importance of hardwoods, palms, and herbs varies depending on local elevation and fire history. In the lower, wetter pinelands the understory tends to have fewer hardwoods and has an herb layer that shares many species with the prairies. Frequently burned sites have better developed herbaceous layers than infrequently burned sites.

Loope et al. (1979) list 186 plant taxa for the rock ridge pinelands, and 67 of these are restricted to pineland habitats. The number of South Florida endemics found in pinelands (32, 17 of which are found exclusively in pineland) is by far the highest for any South Florida vegetation type (Avery and Loope 1980a). All the endemics are herbs except for the shrubs Porestiera segregata var. pinetorum and Lantana depressa (Table 1). South Florida slash pine, although found north of Lake Okeechobee, is endemic to peninsular Florida and the Florida Keys.

The pinelands most similar to those of the Miami Rock Ridge are those of Big Pine Key and several other Lower Keys where the Miami Limestone also outcrops. These pinelands differ mainly in the presence of several tropical hardwoods characteristic of the Florida Keys or nearby coastal areas and the prominence of tree-sized palms of Coccothrinax argentata and Thrinax morrisii (Alexander and Dickson 1972). The pinelands of the Bahama and Caicos Islands are also very similar to those of the rock ridge except that the pine is P. caribaea var. bahamensis (March 1949, Luckhoff 1964, Lamb 1973). The substrate is weathered coralline limestone very much like the oolitic rock of South Florida. Many of the understory species are the same as those found in rock ridge pinelands (Coker 1905, Correll and Correll 1982), although Robertson (1962) noted the conspicuous absence of Serenoa repens. Even though it grows in an ecological

Table 1. Vascular plant taxa endemic to South Florida and found in Miami Rock Ridge (MRR) pinelands, including those of Everglades National Park (after Avery and Loope 1980a).

Taxon	Exclusively in MRR Pinelands	Present in Everglades National Park
<u>Amorpha crenulata</u>	*	
<u>Argythamnia blodgettii</u>		*
<u>Aster concolor</u> var. <u>simulatus</u>	*	
<u>Brickellia mosieri</u>	*	
<u>Chamaesyce conferta</u>		*
<u>C. deltoidea</u> var. <u>adhaerens</u>	*	
<u>C. deltoidea</u> var. <u>deltoidea</u>	*	
<u>C. garberi</u>		*
<u>C. pinetorum</u>	*	*
<u>C. porteri</u> var. <u>porteri</u>	*	*
<u>Croton arenicola</u>		
<u>C. glandulosa</u> var. <u>simpsonii</u>	*	
<u>Dyschoriste oblongifolia</u> var. <u>angusta</u>		*
<u>Evolvulus sericeus</u> var. <u>averyi</u>		*
<u>Forestiera segregata</u> var. <u>pinetorum</u>	*	*
<u>Galactia pinetorum</u>	*	*
<u>G. prostrata</u>	*	
<u>Hyptis alata</u> var. <u>stenophylla</u>	*	*
<u>Jacquemontia curtisiae</u>		*
<u>Lantana depressa</u>	*	*
<u>Linum arenicola</u>		
<u>L. carteri</u> var. <u>carteri</u>		*
<u>L. carteri</u> var. <u>smallii</u>		*
<u>Melanthera parvifolia</u>		
<u>Phyllanthus pentaphyllus</u> var. <u>floridanus</u>		*
<u>Poinsettia pinetorum</u>	*	*
<u>Polygala smallii</u>	*	
<u>Schizachyrium rhizomatum</u>		*
<u>Stillingia sylvatica</u> ssp. <u>tenuis</u>	*	
<u>Tephrosia angustissima</u>	*	
<u>Tragia saxicola</u>		*
<u>Tripsicum floridanum</u>		*

setting virtually identical to that of the rock ridge, P. caribaea var. bahamensis does not have the grass-like seedling stage that characterizes South Florida slash pine. It should be noted that for many years P. elliottii of southeastern U.S. was considered the same species as P. caribaea of the West Indies and Central America (Little and Dorman 1954a,b)

#### Fire Ecology

The rock ridge pineland, like most southern pine forests (Garren 1943), is a fire-maintained vegetation type that develops into hardwood forest in the absence of burning. Robertson (1953) estimated that within 15-25 yr of the cessation of burning, open pine forest would become dense hardwood forest (hammock) under a stand of relic pines; this happened in a small area of pine forest in Everglades National Park that was protected from fires by the construction of a road (see photographs in Wade et al. 1980, p. 93). Alexander (1967) documented the rapid succession of pineland to hammock elsewhere in the rock ridge. The succession to closed hardwood forest results in the elimination of some shrub species and the rich herbaceous flora characteristic of pinelands (Loope and Dunavitz 1981).] This is probably due to the reduction in light reaching the ground but it may also be due in part to the thick accumulation of organic matter that is normally removed by

fires. Loope and Danevitz (1981) found fewer species in a frequently burned pineland than in a pineland unburned for 35 yr.

Fires in pinelands are surface fires that move along the ground consuming litter and understory vegetation. The density of the pine canopy is such that crown fires are unknown, although the trees can be killed by convectional heat under severe burning conditions. Prairies burn readily when sufficient fuels are present but hammocks under normal circumstances do not. Pineland fires usually burn up to the edge of hammocks and go out; however, during extreme droughts the fire may smolder through the hammock, consuming the organic soil and killing the trees. Craighead (1974) suggests that once soil moisture content in hammocks drops to 35% they are susceptible to soil fires.

All the species present in the pinelands are adapted to fires. Mature slash pines are very resistant to fire because of a thick, insulating bark and the relatively heavy buds surrounded by long needles (Hare 1965b, Byram 1948). Both varieties of slash pine are able to recover from 100% crown scorch in some cases (Wade 1983, personal observation). Besides being fire-resistant as an adult, the South Florida slash pine has a fire-resistant seedling stage much like longleaf pine (Little and Dorman 1954a,b). An accidental fire in a plantation of both var. densa and var. elliottii seedlings killed a smaller proportion of the South

Florida variety (Ketcham and Bethune 1963). Seedling establishment is also favored by fires occurring soon before seed fall (Kukla 1973).

The hardwoods in the understory all have the ability to sprout back after being topkilled. Some, such as Phus copallina, are prolific root-sprouters, but most send up new shoots from the rootstock at the base of the stem. Generally, few shrubs are killed completely by single fires. Robertson (1953) recorded mortality of 0-10% in nine species after a fire. Depending on the fuel accumulation and burning conditions, some fires may have no apparent effect on larger hardwoods. All the herbs are perennials that sprout back quickly and seem to flower more profusely in recently burned areas than in unburned areas. Some of this apparent increase in reproductive activity may be due to improved visibility or more synchronous flowering, but there is no question that flowering of many species of grasses is stimulated by burning (Robertson 1962).

The fire history of the rock ridge pinelands is difficult to reconstruct with any degree of detail. The use of fire-scared trees is limited because of the small number of suitable trees and the ambiguity involved in ring counts in South Florida slash pine (Tomlinson and Craighead 1972, Arno and Sneed 1977, Taylor 1980). The only methodology available is to deduce from present-day fire patterns and species attributes what might have occurred in the past.

Lightning fires are a common occurrence today and are likely to have been so ever since the most recent emergence of South Florida from the sea. The lightning is produced during frequent convectional storms during the wet season. The average annual number of lightning strikes reaching the ground in the rock ridge region is 4-10 per km<sup>2</sup> (Taylor 1980). The common sight of single dead pine trees with longitudinal fissures running down their bark is testimony to the high incidence of lightning strikes. In Everglades National Park lightning-caused fires accounted for 28% of all fires and 18% of the park area burned during the period 1948-1979 (Taylor 1981). Almost all these fires occurred within the wet season months of May to October (Fig. 3). During this study (on Aug. 2, 1980) a small lightning fire burned about 3 ha of pineland near one of the sites.

Egler (1952) assumed a low frequency of lightning fires in southern Florida and felt that before the arrival of people the uplands were covered by broad-leaved forest. Robertson (1953, 1954), whose viewpoint seems to be substantiated by more recent estimates of the incidence of lightning-caused fires, felt that the vegetation pattern was much as seen today. He also argued that the presence of pineland endemics implies a long period of existence of this vegetation type. Both agree, however, in suggesting that the arrival of Amerindians about 2000 yr ago (Tebeau 1963) brought about a marked increase in fire frequency and that

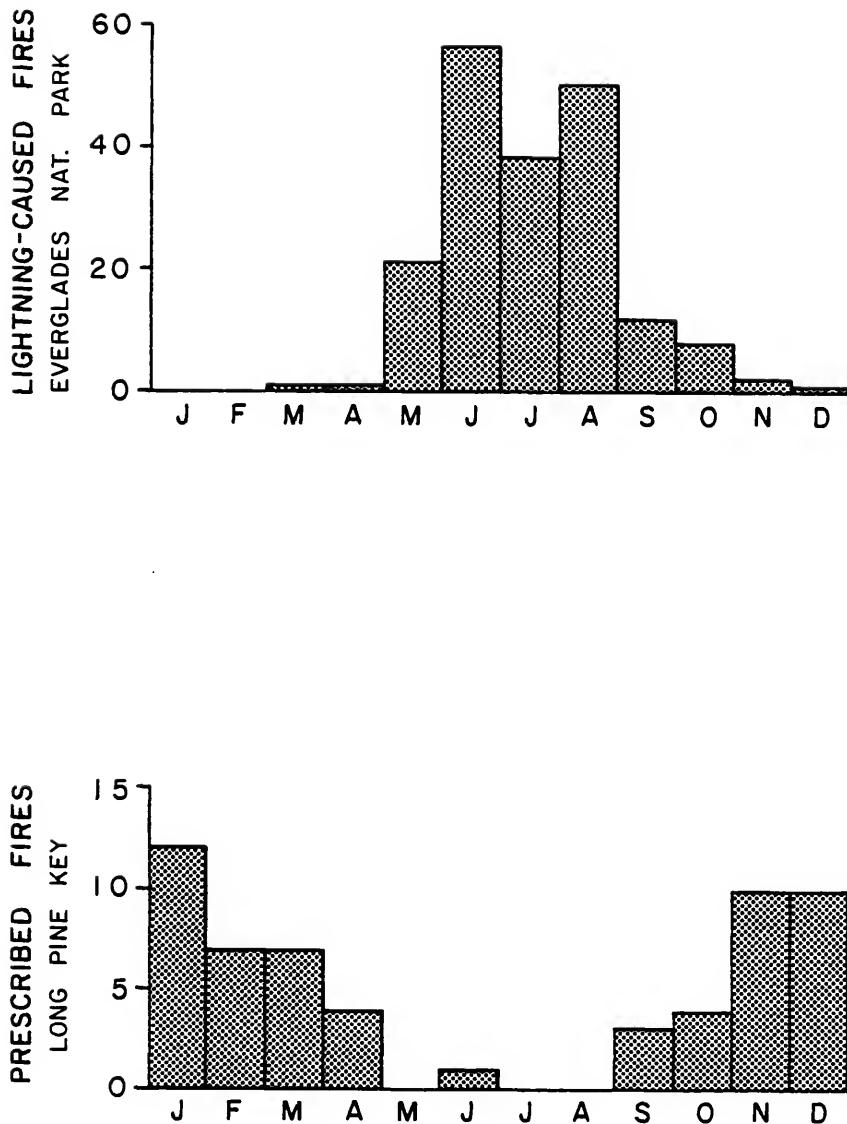


Figure 3. Monthly distribution of lightning-caused fires in Everglades National Park and prescribed fires conducted in Long Pine Key pinelands within the park (after Taylor 1981).

most of these fires probably occurred early in the dry season. The arrival of European settlers on the scene probably resulted in an even higher fire frequency (Robertson 1953, 1954). Besides the obvious effect as an ignition source (or fire suppression agent), modern man has other more subtle effects on the fire pattern. The lowering of water levels by drainage starting in the 1920's has increased the time that many vegetation types are burnable and therefore should increase fire frequency. Lowered water tables also increase the incidence of severe droughts, resulting in more fires in organic soils. On the other hand, roads, canals, and other cultural features form firebreaks that impede the natural spread of fires.

#### Present Extent and Condition

The Miami Rock Ridge pinelands originally covered the rock ridge from Miami to near Mahogany Hammock in Everglades National Park. Davis (1943, see Fig. 2) estimated the original area covered by pine forests to be about 72,900 ha, although he stated that this was certainly an overestimate. The area of the Rockdale soil series can be considered an independent estimate of the original extent of the rock ridge pinelands. This has been given as 66,700 ha (Soil Conservation Service 1958) or 62,800 ha (Leighty et al. 1965).

Today the rock ridge pinelands are almost restricted to the confines of Everglades National Park. A 1975 survey of pinelands and hammocks in Dade County found only 2984 ha of pinelands outside the national park (Shaw 1975). By 1979 the area had dwindled to 2429 ha (Metro-Dade 1979). Most of the pinelands have been destroyed for agriculture or urban development. Only a few areas of pine forest outside of Everglades National Park are likely to be preserved for the foreseeable future. The Dade County Parks and Recreation Department manages three properties with considerable areas of pineland: Larry and Penny Thompson Park (100 ha), Navy Wells Pineland Preserve (100 ha), and the recently acquired Tamiami Pineland Preserve (25 ha) which has sandy soil overlying the limestone (M. Washington, Dade Co. Parks and Rec. Dept., pers. comm.). There are many other smaller parcels of rock ridge pinelands in the southern part of the ridge, but almost without exception they are heavily invaded by *Schinus terebinthifolius*, a weedy exotic tree, and are not properly maintained by prescribed burning (Loope and Dunevitz 1981).

Although the pineland fire management unit of Everglades National Park is about 8000 ha (Everglades National Park 1979), planimetry of a vegetation map of Long Pine Key (Olmsted et al. 1983) and topographic sheets of adjoining areas show that only about 4650 ha are in fact pinelands (T. Caprio, S. Fla. Research Center, pers. comm.). Even within

the park about 500 ha were lost to agriculture before the land was purchased by the federal government (part of the area known as the Hole-in-the-Donut).

Today, therefore, less than 10% of the original rockland pine forest is extant and under some form of management. There is a very strong possibility that many of the plant taxa endemic to the Miami Rock Ridge pinelands will be lost inasmuch as only 8 of 17 are presently found in Everglades National Park (Table 1).

#### Everglades National Park

The pinelands west of Taylor Slough in Everglades National Park, known as Long Pine Key (Fig. 2), are the only major area of rock ridge pinelands remaining today. There is also a small amount of pineland east of Taylor Slough near the main park entrance. The Long Pine Key pinelands are dissected by at least six major transverse prairies and contain more than 100 tropical hammocks. The pineland vegetation is described by Robertson (1953), Loope et al. (1979), and Olmsted et al. (1983).

Everglades National Park was dedicated in December 1947, about the time that the logging of the pine forest begun in the mid-1930's was finished. The pine stands found today are almost entirely second growth, representing the progeny of cull trees. The initial park fire management policy for the pinelands (and the rest of the park as well) was active

fire suppression, in keeping with National Park Service policy. This initially resulted in good regeneration of pine but probably also allowed establishment of large numbers of hardwoods and an increase in size of those already present.

A park service study of fire in the park carried out by Robertson (1953) concluded that fire was needed to maintain pinelands and prevent succession to hammock. This led, in 1958, to Everglades National Park becoming the first park service unit to use prescribed fire. Roads were constructed to divide most of Long Pine Key into ten management blocks. Details of fire management are described by Klukas (1973), Bancroft (1976, 1979), and Taylor (1981) and in the current fire management plan (Everglades National Park 1979). After the initial burns of the management blocks in the late 1950's it was often 10 yr before the next burn; since about 1970 the burning rotation has been shortened to about every 5 yr (Taylor 1981). Until 1980 the prescribed burning of pineland was carried out almost exclusively in the cooler dry season months (Fig. 3). Since then many burns have been carried out during the lightning fire season.

Prescribed burning is used by the park service to reduce fuel loads to "natural" levels and as a substitute for "natural" fire where present-day conditions do not permit the normal pattern of burning (Everglades National Park 1979). A difficulty in carrying out this type of management

is that there is no explicit statement of what constitutes the natural state. Fires caused by indigenous people might be considered as natural as lightning-caused fires.

It is quite possible that the hardwood understory in the pinelands of Everglades National Park is today more conspicuous than it was a hundred years ago. Logging and the subsequent period of fire suppression may have changed the balance between herbaceous and woody species. The prescribed burning program has not significantly reduced the amount of hardwoods from levels present when the program began (Taylor and Herndon 1981).

## CHAPTER II METHODS

### Experimental Design and Site Selection

Paired plots were set up at two sites representative of the rock ridge pinelands of Long Pine Key, Everglades National Park. One randomly selected member of each pair was burned during the wet season of 1980 and the other during the dry season of 1980-81. The burns were intended to be as similar as possible except for air temperature and fuel moisture conditions, which vary seasonally. Aboveground understory biomass and litter were sampled before burning, immediately postburn, and at 2, 7, and 12 mo after burning. The aboveground biomass and nutrient stocks of the regrowth vegetation were taken to be measures of ecosystem recovery.

The sites were chosen to exemplify both the higher, more frequently burned pinelands in the eastern end of Long Pine Key, and the lower, less frequently burned pinelands to the west. The choice was restricted to areas that had been unburned for a long enough period that sufficient fuels for complete burns were present. Pineland management blocks I (site 1) and E (site 2) were chosen as appropriate sites (Fig. 4).

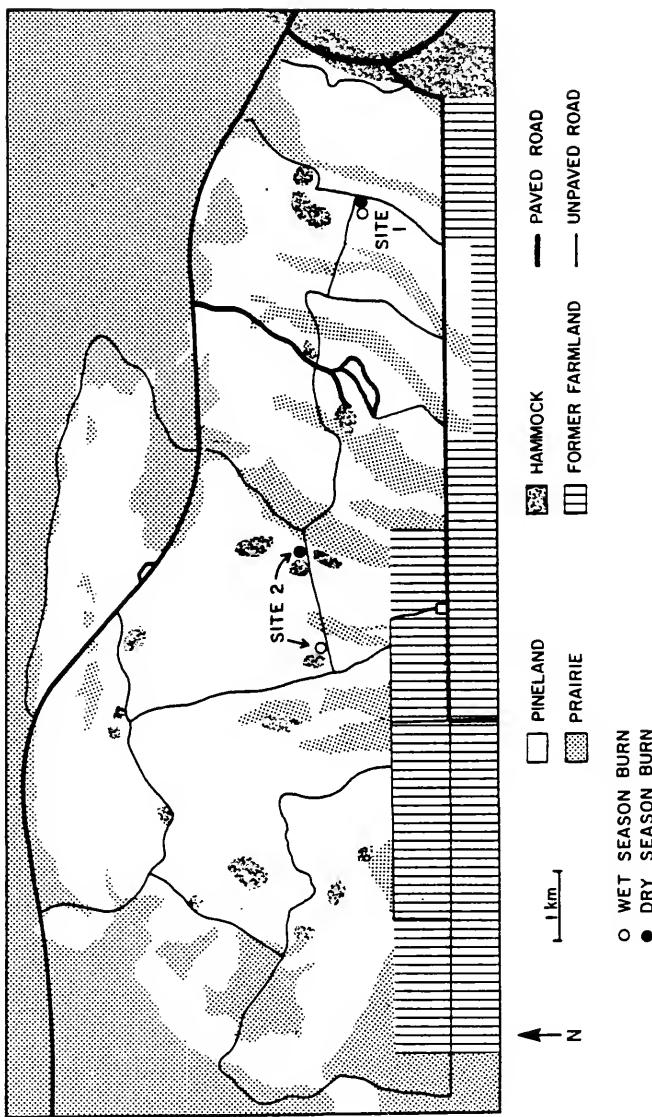


Figure 4. Vegetation map of Long Pine Key, Everglades National Park showing the location of study sites and wet season (open circles) and dry season (closed circles) burn plots. Only the larger hammocks are indicated.

Site 1 contains some of the highest ground in Long Pine Key and had been burned more frequently than any other management block (burns in 8/57, 3/60, 2/63, 12/69, 3/74, and 11/77). The shrub layer at this site was generally below 1.5 m, with few hardwood stems greater than 2 cm basal diameter, and there was a well-developed herb layer. Site 2 was the least frequently burned management block (burned 1/59, 4/69, and 1/75) and is in an area where the water table occasionally reaches the ground surface. The hardwoods at this site were larger, often 2-3 m tall, and basal diameters of 3 cm were common. Solution holes are common in site 2 and there was a less well-developed herb layer than at site 1. The pine canopy at site 1 was made up of larger, more widely spaced trees than those at site 2.

The criteria for plot locations were that they be areas of at least 0.5 ha with relatively homogeneous overstories and understories. The plots (Fig. 4) were located near roads (but > 5 m away) for ease of access and to simplify the development of firebreaks.

#### The Burns

The burns were conducted at least 3 d after a rain when conditions met the criteria of the park fire management plan, including wind direction and air quality standards. Prescriptions were kept broad to insure that the burns could

be done close to the intended date. Fires were set on the leeward sides of the plots because backing fires are more easily controlled and are less likely to cause crown scorch in overstory pines than head or flanking fires. All burns were conducted near midday by the park resource management staff.

Preburn fuels and the material remaining after the burns were collected as part of the biomass and litter sampling. Fine-fuel-moisture samples (material < 7 mm diameter in 0.25 m<sup>2</sup> quadrats) were collected during the burns and dried at 70°C. Relative fire temperatures were measured with plates placed at ground level, 0.5 m, and 1 m on 12 poles at post-burn sampling locations. The plates were made by spotting temperature-sensitive paints (Tempilaq, Tempil Div., Big Three Ind.) on steel plates (75 X 130 X 2.5 mm, 250 g). The paints had melting points of 52, 70, 93, 101, 121, 135, 149, 177, 204, 232, 260, 288, 302, 316, 343, 371, 399, 427, and 454°C according to the manufacturer's specifications (but see Hobbs et al. 1984). The large mass of the plates tends to depress the maximum temperature registered by the melting paints so that they more closely reflect temperatures experienced by the heavier vegetation rather than maximum flame temperatures. The resource management staff measured ambient air temperature, relative humidity, wind direction and speed, and rate of spread. Fireline intensity was calculated by assuming a heat yield of 14,000

kJ/kg of fuel (Wide 1983) and using the following equation (Brown and Davis 1973, Wade 1983):

$$I = Hwr$$

where  $I$  is fire intensity in kW/m,  $H$  is heat yield in kJ/kg,  $w$  is mass of fuel consumed in kg/m<sup>2</sup>, and  $r$  is rate of spread of fire front in m/s.

#### Aboveground Mass Sampling

##### Vegetation and Litter

Aboveground understory vegetation and litter were destructively sampled for dry mass. The sampling was done in 60 X 80 m plots (0.48 ha) subdivided into 12 20 X 20 m subplots. Within each subplot, potential sampling quadrats were arranged in a grid pattern. At site 1 there were 16 2 X 2 m quadrats and at site 2, nine 3 X 3 m quadrats available per subplot. At each sampling period two randomly chosen quadrats per subplot were sampled at site 1 and one quadrat per subplot at site 2. Therefore, approximately equal areas were sampled in both sites, but larger quadrats in site 2 plots were used to reduce between-quadrat variance. Buffer strips 3 m wide between quadrats permitted movement through the plots without disturbing sampling sites.

All plants were clipped at ground level except palms which were clipped at the base of the petioles. In Long

Pine Key Sabal palmetto and Coccothrinax argentata usually have little stem projecting above ground, and although the horizontal, creeping rhizome of Serenoa repens is often on top of the rock substrate, it is generally unaffected by fire and is functionally much like a belowground structure. Shrubs and palms were collected from the entire quadrat. Herbs and litter were harvested only from 1 x 1 m quadrats nested in the NW corner of the larger shrub quadrats. In the site 2 plots, herbs and litter were sampled from an additional 1 x 1 m quadrat in the SE corner of the shrub quadrat beginning with the 2-mo postburn sampling. Pine seedlings were counted in the herb and litter quadrats.

Litter was defined as any dead plant material identifiable as to origin, essentially the L and F forest floor layers of the older forest soils literature (Pritchett 1979). Generally there is little humus material (H layer) present in Long Pine Key pinelands because of frequent fires, but in site 2 especially there were occasional pockets of well-decomposed plant matter. A prominent part of the litter after a fire in these pinelands is the standing dead hardwood stems; these were sampled from the entire shrub quadrat. Dead palm fronds were included with forest floor litter in the 1 x 1 m quadrats as were any pine needles draped in the understory vegetation.

The harvested material was sorted into various compartments, dried at 70°C to constant mass, and weighed to

0.1 g. Shrubs were sorted by species; leaves (plus rarely occurring reproductive parts) were separated from stems for the preburn, postburn, and 12-mo sampling periods. Petioles were not separated from blades of palm leaves. Herbs were treated as a single compartment although record was kept of all species observed in each plot. Litter was separated into pine and non-pine components. In the preburn sampling only subsamples of litter were separated and the proportions were applied to total dry mass. At later sampling periods pine litter was further subdivided into needles and other pine and the non-pine litter was categorized as herb litter, forest floor shrub litter, and standing dead.

For nutrient analysis, vegetation and litter from three adjacent subplots were bulked by type and a large subsample kept. In general the categories were the same as those recorded for mass, except that only two or three of the most important shrub species in a given set of subplots were kept separate and the rest were combined.

The diameters at 1.5 m (dbh) and height of all pine trees in each plot were recorded along with the number of standing dead trees (snags) and stumps. Regression equations from the literature were used to estimate biomass of the overstory.

Postburn Ash

Accounting for the mass and nutrient content of the ash following the fires posed a special methodological problem. The ash was collected by two methods. The first consisted of placing four Petri dish bottoms (9 cm dia., 20 mm depth) under the litter before the burn at 12 postburn sampling locations (one in each subplot). Immediately after the fire, covers were put on the dishes and they were taken back to the lab. The contents of the four dishes from each location were combined to form a single sample. The advantage of this method is that the samples can be collected as soon as the fire front passes; a sudden rain does not preclude sampling. The disadvantages are the relatively small area sampled and the difficulty in placing the dishes under all the fuel, especially in an area with a substrate as rough as Miami oolite.

The second method was to pick up the ash with a small vacuum (Car-Vac, Black and Decker) powered by a 12 V battery. At the same 12 postburn sampling locations a 0.2 m<sup>2</sup> area was vacuumed and the material was transferred to plastic bags. This method cannot be used once the ash is wetted. It is very effective at picking up all the ash, but there is potential for contamination with soil. Both types of ash samples were analyzed individually for nutrient content, although N was measured only in the vacuum samples.

### Litterfall

The contribution of the pine overstory to understory littermass and nutrients was measured by collecting litterfall for the 12 mo post-fire period. Pine needles, bark, and male cones were collected in litter trays (galvanized greenhouse flats, 0.187 m<sup>2</sup>, with drainage holes) placed two per subplot in each of the treatments. Trays were also put out in an unburned area of site 2 to see if burning increased needlefall. The trays were emptied at 2-5 wk intervals and material from three adjacent subplots was pooled to give four samples per plot. The litter was oven dried (70°C), sorted into needles and other fine pine material, and weighed to 0.1 g. All other material was discarded. The input of larger material which is inadequately sampled by litter trays (branches and seed cones) was measured separately at both sites. All newly fallen (uncharred) material was picked up from a strip 2.5 m wide outside the dry season burn plot borders twice during the year after burning. Collecting was done in 20 m lengths, resulting in 14 50 m<sup>2</sup> sampling areas. Branches were separated into 1-cm diameter classes before oven drying and weighing. I assumed that branch and seed cone litterfall was the same at both plots in a given site.

Needlefall was bulked by plot for a dry season period (Dec.-Jan.) for nutrient analysis because these samples were least subject to leaching losses while in the litter trays.

The total annual fine litterfall (mostly bark) was bulked by plot for analysis. The nutrient content of branches and seed cones was measured on material that fell during a 77 d period during the dry season at the site 2 dry-season plot. Materials from the (three or four) sampling areas on each side of the plot were combined and subsampled to give four samples of each type. The nutrient concentrations of the 2-3 cm branch class were applied to the small amount of material larger than 3 cm diameter.

#### Soil Sampling

Two types of soil samples were collected to characterize the surface soil (0-7.5 cm) and to detect changes in soil properties present 12 mo after burning. The first type was samples taken from the preburn biomass quadrats in all the plots and from the 12-mo quadrats in two of the plots. Ten scoops were taken with a trowel in each subplot and then bulked to form 12 samples per plot. The sampling spots were spaced as evenly as possible in each quadrat, but considerable searching in cracks and crevices was often required before a scoopful of soil was found.

At site 1 areas of reddish-brown mineral soil were encountered in the preburn soil sampling; these areas were readily apparent after the burns. The extent of these pockets of "Redland" soil in the site 1 plots was estimated by line-intercept along the 20 m borders of all subplots

(n=31 in each plot). Because the preburn soil samples were heterogeneous with respect to the type of soil sampled, a second sampling restricted to the Redland soil was done. Composite samples of 10 scoops of mineral soil from throughout each of the subplots in the site 1 dry season plot were taken 12 mo after the burn. In the adjacent area which burned 5 yr previously composite samples were collected in a similar manner along 10 m segments of a 120 m transect. All the soils were dried (70°C) and sieved (2 mm screen) before analysis.

#### Tissue and Soil Analysis

Subsamples (0.5-1 L) of the bulked vegetation and litter material for chemical analysis were ground in a large Wiley mill, thoroughly mixed, and stored in polyethylene bottles. The ground samples were redried at 70°C before weighing. Cations (Ca, Mg, and K) and P were measured on 1,000 g samples placed in 50 ml Pyrex beakers and ashed at 500°C for at least 3 hr. The residue was dissolved and then brought to dryness first with 5N HCl and then concentrated HCl before filtering (Whatman No. 42) and bringing to 50 ml final volume with 0.1N HCl. Calcium and Mg concentrations were determined by atomic absorption, K by flame emission, and P by automated colorimetry (Mitchell and Rhue 1979). Nitrogen was analyzed by a micro-Kjeldahl procedure using 0.500 g of litter and stem tissues and 0.250 g of all other

materials. Ammonium was determined by automated colorimetry (Anonymous 1977). The cation and P content of the postburn ash was determined by similar methods except that the residue after ashing was dissolved in larger (10X-20X) volumes of acid because of much higher nutrient concentrations. Following Kjeldahl digestion of the ash, ammonium was measured by distillation and titration.

As a check on analytical procedures, replicates of a single leaf tissue sample were run with each set of dry-ashed samples. The replication was good, with coefficients of variation of 4.0%, 3.5%, 3.0%, and 2.4% for K, Ca, Mg, and P, respectively. Recovery of K, Ca, and P from four samples of National Bureau of Standards pine needle tissue averaged 81%, 118%, and 98% of the values listed for these elements. There is no published value for Mg. The N.B.S. pine needle tissue was run with each set of Kjeldahl analyses and always was within 3% of the nominal value.

Soil pH was measured in a slurry of 25 ml of soil and 50 ml of water equilibrated for 30 min. Organic matter was measured by the Walkley-Black wet oxidation method on 1.0 g samples. Cations and P were extracted by the double-acid (0.05N HCl - 0.025N Na<sub>2</sub>SO<sub>4</sub>) method and analyzed as for plant tissues. Details of methods are found in Mitchell and Phu (1979).

CHAPTER III  
RESULTS

Initial Vegetation Structure

*Pinus elliottii* var. *densa* was the sole canopy tree species in all the plots. Both sites had apparently been logged not long before the establishment of the park; numerous stumps still remaining have resisted more than 40 yr of exposure and several fires. The density of pine trees at site 1 was about half that at site 2, but the mean basal area per tree was about twice as large, so total basal area at the two sites was similar (Table 2). The trees at site 1 were also taller than those at site 2. Many of the larger pines at site 2 had misshapen crowns and probably represent cull trees.

There were very few pine saplings (< 5 cm dbh) at site 2 and none at site 1 (Figs. 5-7). There were also very few pines <1.5 m tall that had grown out of the "grass" stage at either site. Before the burns site 1 had 1.2-1.5 seedlings (no stem elongation) per m<sup>2</sup> and site 2 had 0.1-0.3 (Table 10).

A total of 129 taxa were observed in the plots during the course of the study (Table 3, Appendix A). This is a slight underestimate of the number of species present because some

Table 2. Characteristics of the pine overstory at the four 0.48 ha study plots.  
 Canopy height is mean of tallest tree in each of the 12 subplots.

Site	Plot (Burn season)	Tree density (no./ha)	Total basal area (m <sup>2</sup> /ha)	Mean basal area (m <sup>2</sup> /tree)	Modal dbh class (cm)	Canopy height (m)	Standing dead trees (no./ha)	Stumps (no./ha)
1	Wet	604	17.8	0.029	21-21.9	23.5	31	173
	Dry	458	16.0	0.035	22-22.9	24.6	25	92
2	Wet	1133	16.3	0.014	9-9.9	19.2	35	88
	Dry	1179	18.1	0.015	9-9.9	19.9	27	65

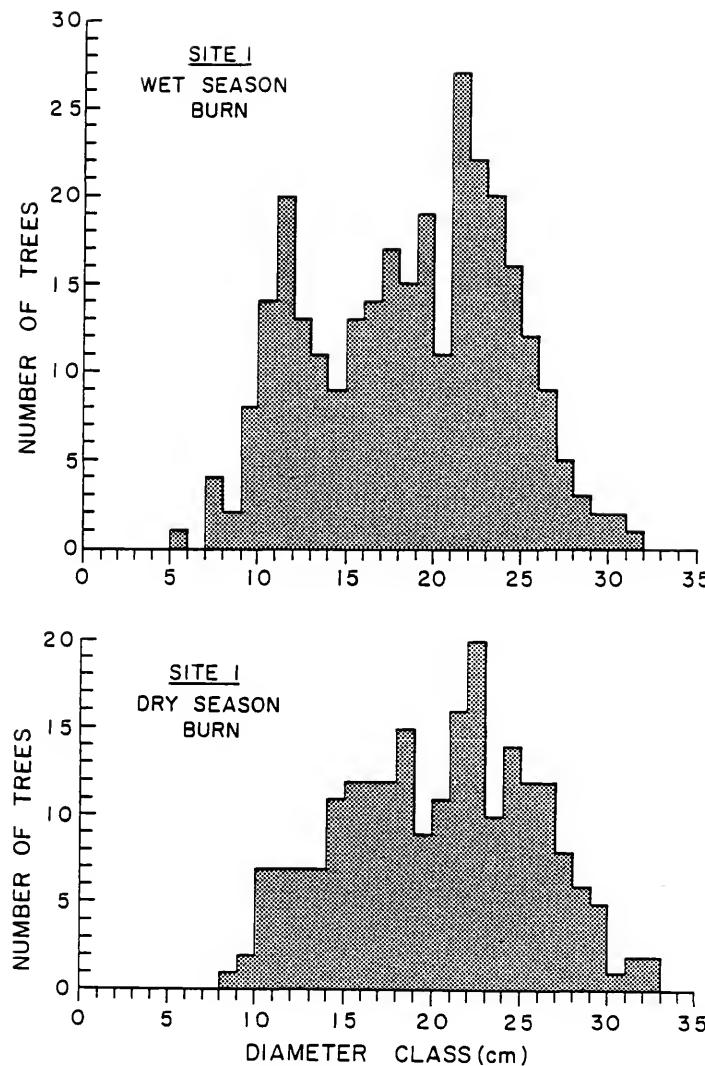


Figure 5. Size-class distribution of pine trees in the site 1 plots.

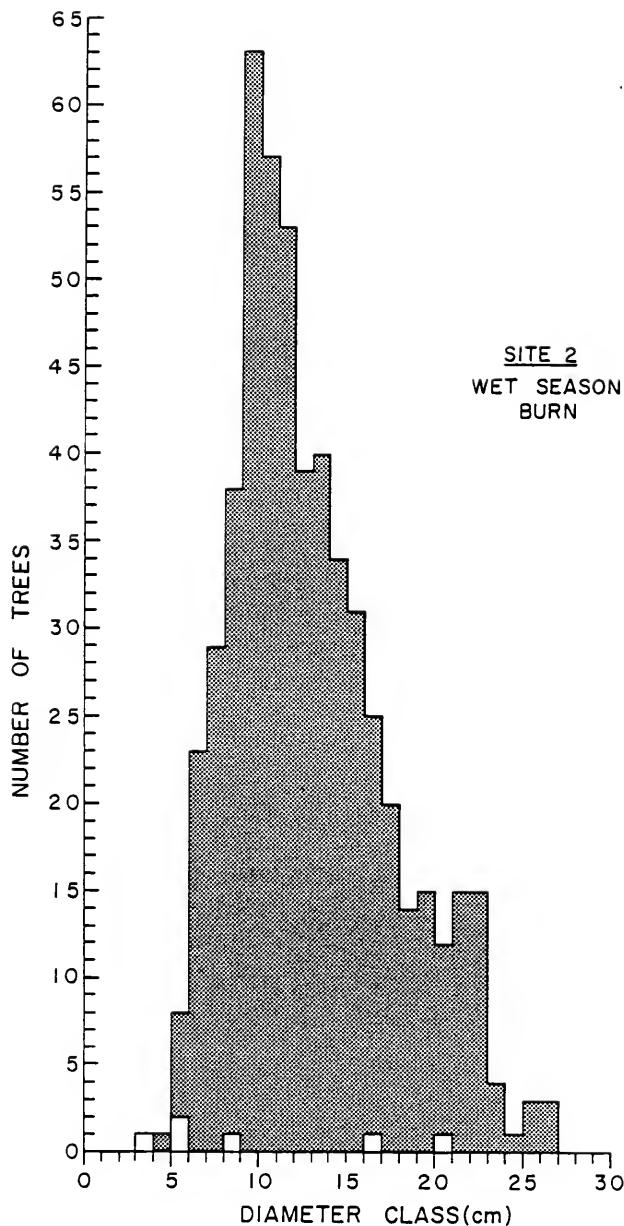


Figure 6. Size-class distribution of pine trees in the site 2 wet season burn plot. Unshaded bars represent trees dead at 1 yr postburn.

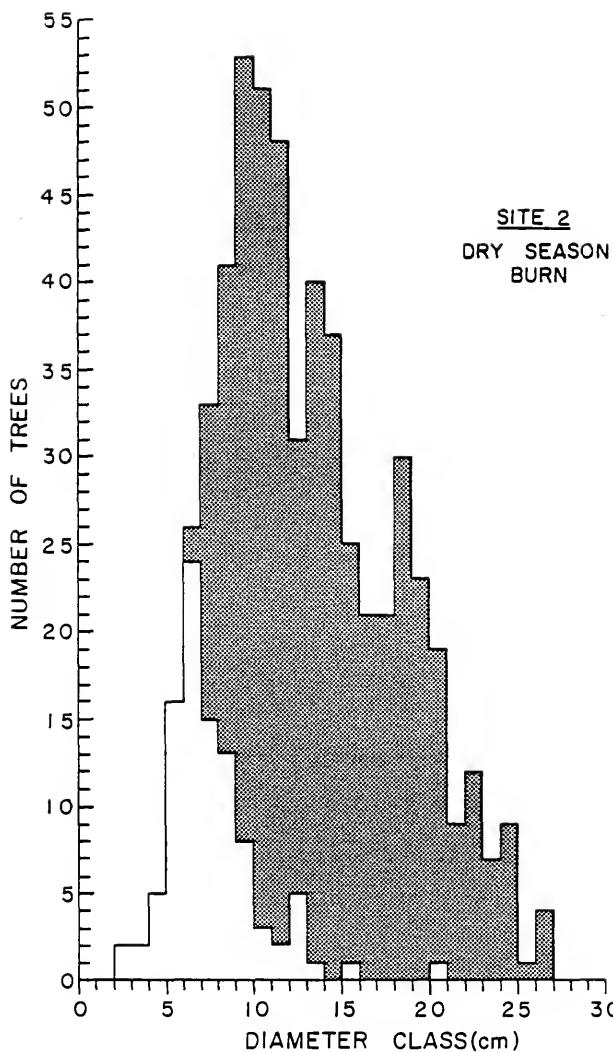


Figure 7. Size-class distribution of pine trees in the site 2 dry season burn plot. Unshaded bars represent trees dead 1 yr postburn.

Table 3. Number of vascular plant taxa found in the understorey of the four 0.48 ha study plots, summarized from Appendix A. Does not include *Pinus elliottii* var. densa.

Category	Site 1		Site 2		
	Wet season burn plot	Dry season burn plot	Wet season burn plot	Dry season burn plot	All plots
<b>Herbs</b>					
Ferns	3	3	3	4	4
Monocots	12	14	11	8	16
Dicots	41	47	37	39	55
Total	56	64	51	51	75
<b>Shrubs</b>					
Cycads	1	1	0	1	1
Palms	3	3	2	3	3
Hardwoods	27	34	42	39	49
Total	31	38	44	43	53
Understory total	87	102	95	94	128

uncommon species were probably missed and because a few herbs were identified only to genus. Within the herbs the Asteraceae, Poaceae, Euphorbiaceae, and Fabaceae were particularly well represented. Five shrub species are members of the Rubiaceae, which contributes an additional four herb species. Other important shrub families reflecting the tropical origins of the flora include the Arecaceae (palms, 3 spp.), Anacardiaceae (4 spp., including one exotic), Sapotaceae (3 spp.), and Myrtaceae (3 spp.).

The overall species richness did not vary much between sites; however the site 1 plots had higher herb species richness and the site 2 plots had higher hardwood species richness. This pattern may be due to characteristics of the substrate and the close association of the site 2 plots with hardwood hammocks that can serve as seed sources; it could also be due in part to more frequent burning of site 1. Some herbs in site 2 are restricted to the wetter microhabitats in solution holes (e.g. Cladium jamaicense and Thelypteris kunthii) and some grasses and sedges at site 1 seem to be found only in the patches of Redland soil (e.g. Rhynchospora globularis and Desmodium lineatum). The hardwood species found in site 2 and not in site 1 are mostly species characteristic of lower, wetter areas (e.g. Chrysobalanus icaco and Ilex cassine) or species found in nearby hammocks (e.g. Coccoloba diversifolia and Lysiloma latisiliqua).

The pine overstory clearly dominates the vegetation in terms of biomass (Table 4). The understory vegetation, in which the hardwoods are the dominant component, made up 6% or less of the total aboveground biomass. The understory vegetation is much more important in terms of nutrient content because so much of the overstory biomass is wood, which has low nutrient concentrations.

Although herb species richness was due largely to forbs species, graminoids in general contributed more to herb biomass. Prominent grasses include Schizachyrium rhizomatum (a South Florida endemic) and Andropogon cahanisii. The major exception to this was occasional patches dominated by the fern Pteridium aquilinum at site 1. The relative dominance of the understory shrub species as expressed by percent biomass is shown in Figure 8. Guettarda scabra was the dominant species at both sites, but less so at site 2 where there were more species. At site 1 Dodonaea viscosa was the second most important species, a position held by Myrica cerifera at site 2. At site 1 the top two species account for about 55% of the shrub biomass, and at site 2 only 41%. The palms Sabal palmetto and Serenoi repens are among the top ten species at both sites, but S. repens is more important at site 1 and S. palmetto at site 2. Coccothrinax argentata is rare at site 2 and is much less important than the other two palms at site 1. The biomass relations of the palms are a reflection of their densities

Table 4. Preburn aboveground vegetation dry mass ( $\text{g/m}^2$ , mean  $\pm$  standard error) at the four study plots.

Category	Site 1		Site 2	
	Wet season burn plot	Dry season burn plot	Wet season burn plot	Dry season burn plot
Herbs	41 $\pm$ 3.8	30 $\pm$ 3.2	22 $\pm$ 5.6	19 $\pm$ 4.0
Shrubs	194 $\pm$ 15.5	170 $\pm$ 14.6	434 $\pm$ 31.8	472 $\pm$ 83.0
Palms	42 $\pm$ 8.1	39 $\pm$ 10.4	39 $\pm$ 6.8	43 $\pm$ 10.4
Hardwoods	152 $\pm$ 17.3 <sup>a</sup>	131 $\pm$ 11.6 <sup>a</sup>	395 $\pm$ 34.2	429 $\pm$ 83.8
Total Understory	235 $\pm$ 15.0	200 $\pm$ 14.0	456 $\pm$ 31.3	491 $\pm$ 81.4
Pine Overstory <sup>b</sup>	8859	8184	7007	7772
Grand total	9094	8384	7463	8263

<sup>a</sup>Includes small amount of *Zamia floridana*.

<sup>b</sup>Based on plot inventories and regression equations for *Pinus elliottii* var. *elliottii* in northcentral Florida (Swindel et al. 1978).

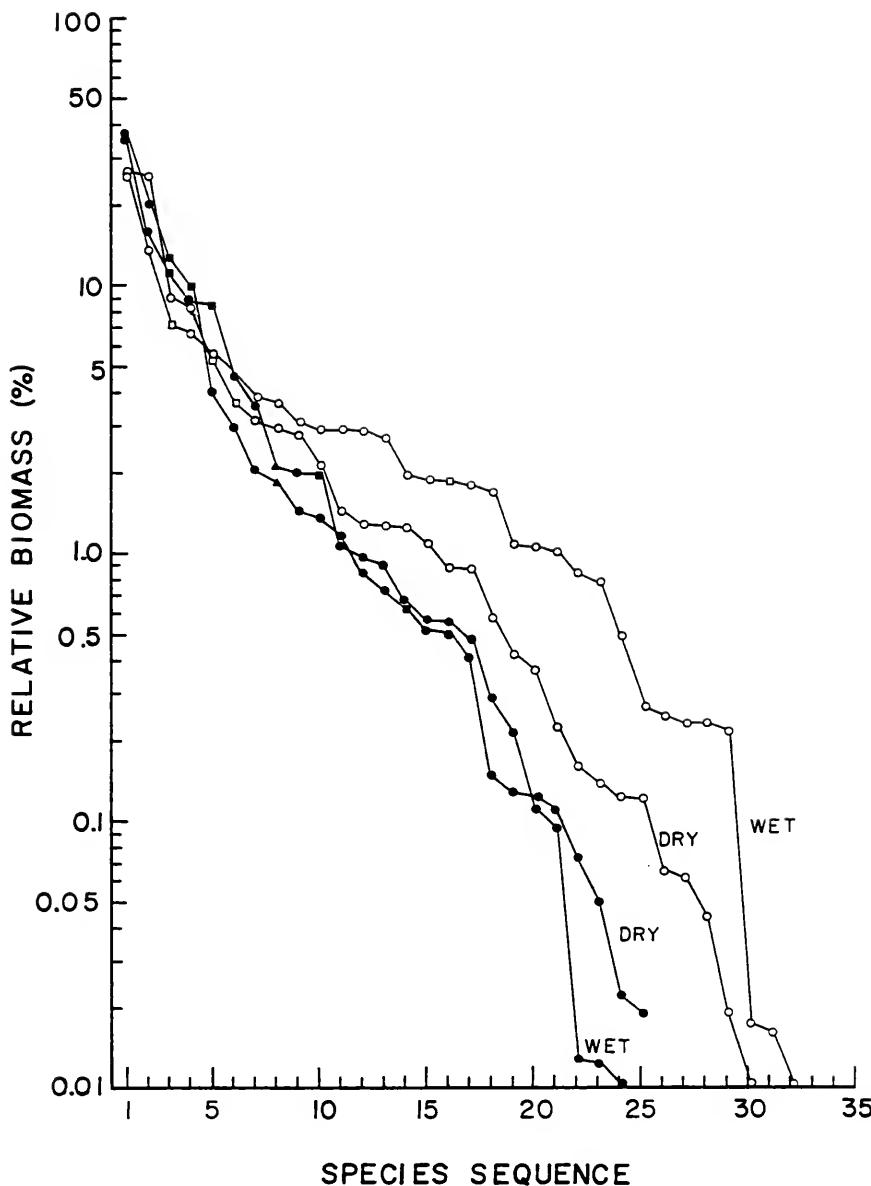


Figure 8. Dominance-diversity curves for preburn shrubs in the study plots. Circles = hardwoods, squares = palms, and triangles = Zamia floridana. Site 1 plots are represented by closed symbols and site 2 plots by open symbols.

at the two sites (Table 5). *Zamia pumila* had the eighth highest preburn biomass at site 1 but was rare at site 2.

#### Burn Descriptions

The wet season burns were carried out under conditions of relatively high ambient temperatures and humidities, although the fuel moisture of the site 1 wet season plot was as low as the dry season plot (Table 6). The site 2 wet season fuel was much moister than the dry season fuel.

All four burns resulted in 100% topkill of the understory vegetation, with minimal canopy scorch. About 70% of the fuel was consumed in the burns except for the site 2 wet season burn in which high moisture content reduced consumption to about 50%. The ash resulting from the burns formed a thin, discontinuous layer on the rock surface until the first postburn rain washed it away.

The rate of spread of the fire front was less than 1.5 cm/s except for brief head fires during wind shifts in the site 1 dry season burn. The intensity of the burns was within the optimum range for prescribed fires (73-260 kW/m, Wade 1983) except for those brief periods in the site 1 dry season burn that resulted in the scorching of about 10% of the crowns.

The average fire temperatures registered by the temperature-sensitive paints varied significantly among the burns (Table 6). The site 2 dry season burn, where the

Table 5. Density of palms (no./ha) in the study plots. Based on counts from preburn and 2-, 7-, and 12-mo postburn sampling quadrats. For Serenoa the value reflects the number of stem apices, whether connected by rhizome or not. Seedlings with juvenile leaves are not included.

Species	Site 1		Site 2	
	Wet season burn plot	Dry season burn plot	Wet season burn plot	Dry season burn plot
<u>Coccothrinax argentata</u>	234	78	0	0
<u>Sabal palmetto</u>	495	495	1968	2060
<u>Serenoa repens</u>	11693	2292	1065	1296
Total	2422	2865	3033	3356

Table 6. Description of the four experimental burns. Values separated by hyphen show ranges, values separated by comma denote individual measurements. Burn temperatures are median (and range) of maximum temperatures of 9-12 plates (see Methods). Within a column values with different superscripts are statistically different at  $p = 0.05$  (Kruskal-Wallis followed by multiple comparison [Conover 1980]).

Site	Burn season	Date of burn	Time since last burn (mo)	Time since last rain (d)	Air temperature (°C)	Relative humidity (%)	Fine fuel moisture (% dry mass)	Wind direction	Wind speed (km/hr)
1	Wet	8-9-80	42.5	6	31-34	61-67	20.5 <sup>a</sup>	E-SE	0-10
	Dry	1-20-81	48	>21	21	56-58	18.0 <sup>a</sup>	SE-SW	0-8
2	Wet	9-19-80	68	4	32-33	62-65	32.5 <sup>b</sup>	E	3-11
	Dry	3-4-81	74	14	27	54-56	16.9 <sup>a</sup>	SE	2-8

Site	Burn season	Burn temperature (°C)			Preburn fuel mass (g/m <sup>2</sup> )	Fuel consumption (g/m <sup>2</sup> )	Rate of spread (cm/s)	Fire line intensity (kW/m)
		Ground level	0.5 m	1.0 m				
1	Wet	31.6 <sup>a</sup> (204-343)	23.2 <sup>b</sup> (135-316)	13.5 <sup>bc</sup> (111-232)	1416	1036 (73%)	0.7,1.0	102,145
	Dry	23.2 <sup>b</sup> (204-316)	20.4 <sup>bc</sup> (149-343)	14.9 <sup>b</sup> (121-177)	1333	948 (71%)	1.4,3.1	186,411
2	Wet	26.0 <sup>b</sup> (149-343)	17.7 <sup>c</sup> (93-32)	12.1 <sup>c</sup> (52-149)	1909	979 (51%)	0.7	96
	Dry	34.3 <sup>a</sup> (260-343)	31.6 <sup>a</sup> (204-343)	20.4 <sup>a</sup> (145-316)	1976	1450 (73%)	1.0,1.2	203,244

greatest amount of fuel burned, had the highest temperatures; however, the ground-level temperature was not significantly different from the site 1 wet season burn. The ground-level temperature of the site 1 dry season plot was lower than the wet season plot, probably because of lower ambient temperatures and the more rapid movement of the fire over the plot. Temperatures decreased with height above the ground, although this pattern was least pronounced at the site 1 dry season burn.

#### Fire Effects on Understory Mass and Nutrients

##### Initial Distribution of Mass and Nutrients

The relative distribution of the preburn fuel mass among live understory vegetation, understory litter, and pine litter was similar in all four plots (Figs. 9 and 10). Pine litter accounted for 50-70% of the mass and live vegetation for 25% or less. The distribution of N and Ca was similar to mass, but Mg, P, and especially K were relatively high in the live vegetation. In fact, 75-80% of the K in the fuel was contained in the live vegetation. Potassium is easily leached and quickly lost from dead tissues. Within the live vegetation hardwood shrubs were responsible for > 50% of the mass and nutrients, more so at site 2 which had not burned for a longer time.

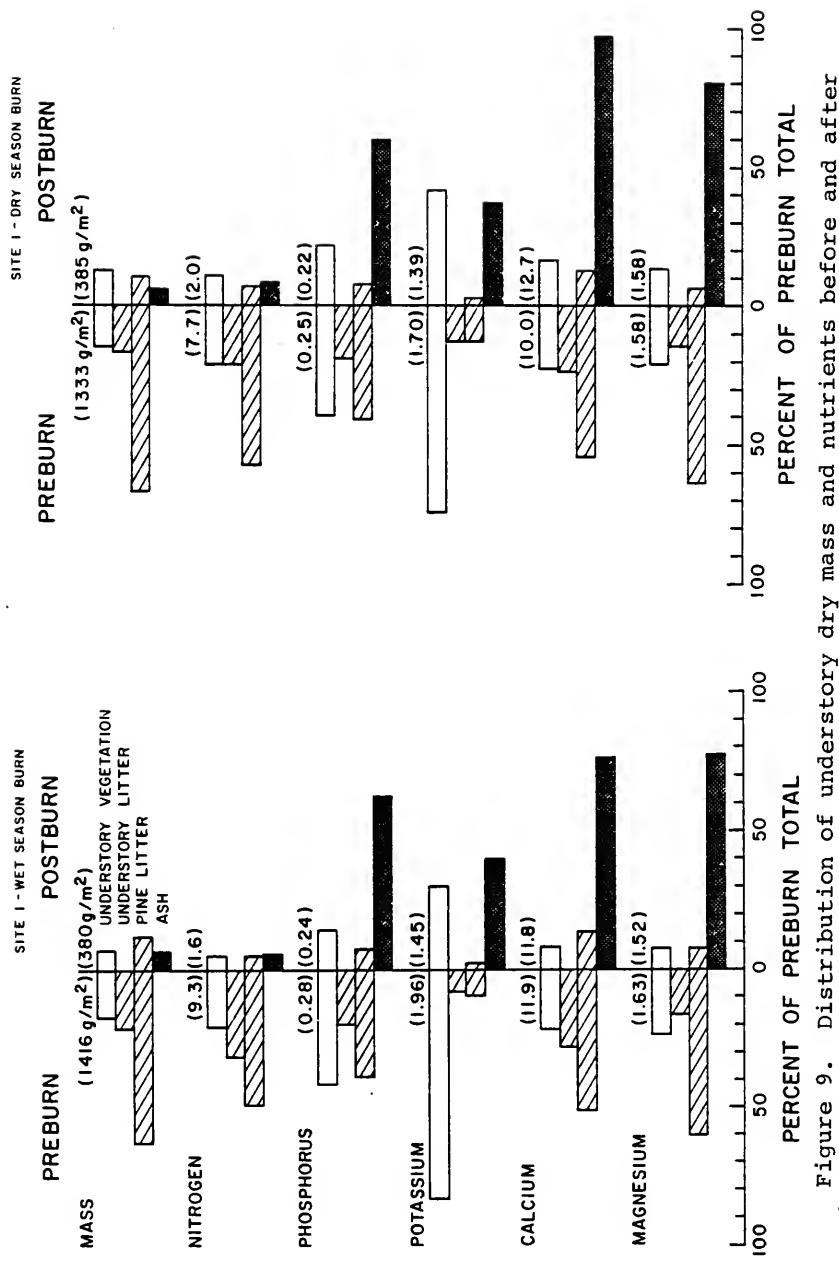


Figure 9. Distribution of understory dry mass and nutrients before and after burning--site 1 burns.

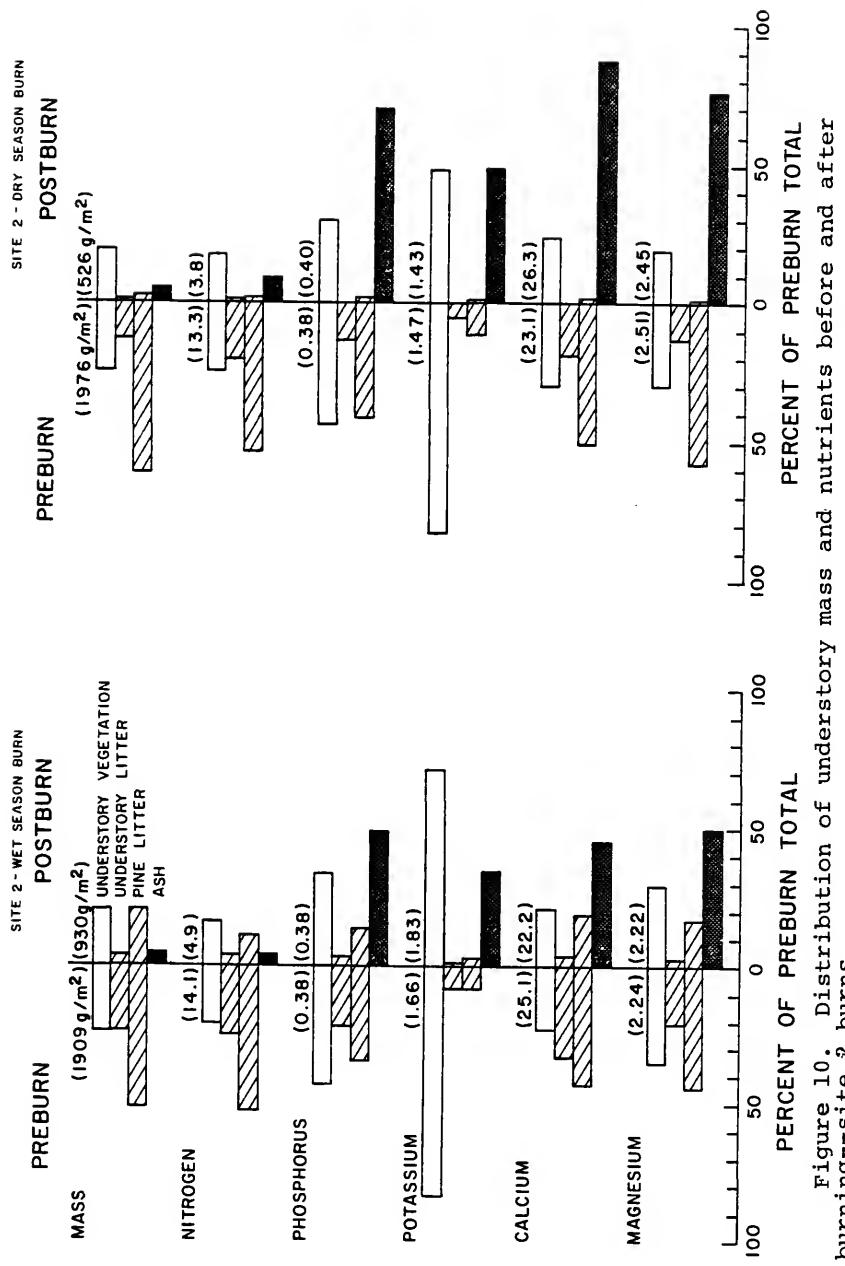


Figure 10. Distribution of understory mass and nutrients before and after burning--site 2 burns.

### Ash Collection Methods

There were no significant differences between postburn ash collection methods for mass, nutrient concentrations, or nutrient standing crops in the site 1 burns with a single exception: higher Mg concentration by the Petri dish method from the dry season burn (Table 7). There was, however, a consistent pattern of higher mean nutrient concentrations in the ash collected by the petri dish method. A light rain falling near the end of the site 2 wet season burn precluded the collection of ash by the vacuum method for that burn. In the site 2 dry season burn the estimates of ash mass and all nutrient standing crops were significantly higher for the vacuum method. The tendency for higher nutrient concentrations in the petri dish ash was also found here, with only Mg significantly higher. Apparently at site 2 substantial amounts of unburned humus and/or mineral soil were picked up by the vacuum. This would account for both the higher mass and the tendency toward lower nutrient concentrations. Because of the larger surface area sampled by the vacuum method, it produced smaller coefficients of variation for mass and nutrient concentrations in 14 of 15 cases.

The dry mass and nutrient (cations and P) values from the petri dish method were used to estimate postburn standing crops because they were available for all the burns and because vacuum samples gave over-estimates at site 2.

Table 7. Postburn ash summary. Differences between ash collection methods shown with asterisks (\* p = 0.05, \*\* p = 0.01; t-test, n = 12).

Site	Burn season	Ash sampling method	Dry mass (g/m <sup>2</sup> )	Residue (% dry mass)	Nutrient concentration (% dry mass)			
					N	P	K	
							Ca	Mg
1	Wet	Petri	96±18.6	53.6±4.78	--	0.250±0.0353	1.13±0.198	11.0±0.93
		Vacuum	95±10.2	48.5±1.58	0.574±0.0417	0.219±0.0174	1.03±0.104	10.6±0.94
1	Dry	Petri	78±16.0	47.1±3.36	--	0.210±0.0122	0.88±0.118	15.5±2.69
		Vacuum	93±7.4	47.7±2.66	0.698±0.0248	0.234±0.0233	0.85±0.060	11.0±0.79
2	Wet	Petri	84±4.9	42.4±1.86	--	0.223±0.0092	0.69±0.084	13.5±0.74
2	Dry	Petri	92±8.3	64.4±3.88	--	0.315±0.0247	0.81±0.104	22.2±1.47
		Vacuum	170±11.2	55.8±1.89	0.713±0.0300	0.259±0.0132	0.70±0.056	18.9±0.87
Site	Burn season	Ash sampling method	Nutrient mass (g/m <sup>2</sup> )					
			N		P		K	
							Ca	Mg
1	Wet	Petri	--	0.176±0.0188	0.79±0.100	9.1±1.33	1.27±0.170	
		Vacuum	0.56±0.090	0.198±0.0174	0.94±0.103	9.5±0.92	1.20±0.127	
1	Dry	Petri	--	0.151±0.0170	0.63±0.060	9.7±1.48	1.27±0.170	
		Vacuum	0.65±0.055	0.192±0.0149	0.80±0.084	10.2±1.08	1.15±0.084	
2	Wet	Petri	--	0.185±0.0099	0.56±0.053	11.2±0.52	1.12±0.078	
2	Dry	Petri	--	0.266±0.0322	0.71±0.093	20.1±2.30	1.92±0.164	
		Vacuum	1.22±0.104	0.437±0.0324	1.18±0.103	32.0±2.58	2.58±0.151	

Nitrogen in ash was estimated from the mass and nutrient concentration data collected by the vacuum method. Since these data were not available for the site 2 wet season burn, the mean N concentration for the site 2 dry season burn was applied to the wet season petri dish estimates of ash mass. The estimate of N in the postburn ash at the site 2 dry season burn is undoubtedly an over-estimate and therefore gives a conservative estimate of the loss of N for that burn.

#### Postburn Distribution of Mass and Nutrients

Most of the litter (except for the heavier pine branches and cones) was consumed in all the burns (Figs. 9 and 10); in the site 2 wet season burn considerable amounts of the partially decomposed lower layers of litter in depressions were also left. Most of the preburn vegetation did not burn except in the site 1 wet season burn where slightly more than half was consumed. Herbs were almost completely consumed in the burns (except for petioles of *Pteridium*), but shrub stems and most leaf material remained. The shrub stems that remained upright became the standing dead compartment of the postburn litter. The blades of palm fronds were often at least partially consumed but the petioles did not burn. The 78-95 g/m<sup>2</sup> of postburn ash accounted for 9-25% of the mass remaining after the burns.

The losses of nutrients from the litter and vegetation were roughly proportional to the losses in mass (Figs. 9 and 10). One-half or more of the standing crops of the non-volatile elements other than K were found in the ash after the burns. A large proportion of the K remained in the dead, but unconsumed, vegetation (mostly shrubs). The postburn distribution of N was similar to the postburn distribution of mass.

The overall losses of organic matter from the ecosystem ranged from about 1-1.5 kg/m<sup>2</sup> (Table 8). The losses of N ranged from 5.7-9.5 g/m<sup>2</sup>. There were no significant differences between preburn and postburn standing crops of the non-volatile elements except for a loss of K in the site 1 wet season burn. This represents one of 16 tests (at 0.05 level) for nonvolatile nutrients and may be a false rejection (i.e., a type I error). There is little reason to expect detectable losses of K in relatively cool fires such as these.

#### Postfire Recovery of Mass and Nutrients

##### Vegetation

Although aboveground plant parts were killed by the burns, I observed almost no plant mortality. One of the most striking features of the postburn period was the rapid reappearance of green tissues, especially herbs and palms. Within days after the burns fresh blades of grass appeared

Table 8. Preburn and postburn standing crops of dry mass and nutrients in the understory; including vegetation, litter, and ash ( $\text{g/m}^2$ , mean  $\pm$  standard error). Statistically significant losses ( $p = 0.05$ , paired t-test,  $n = 4$ ) shown by asterisk.

Dry mass or nutrient	Site 1			Site 2		
	Wet	Dry	Wet	Dry	Wet	Dry
Dry mass						
Preburn	1416 $\pm$ 52	1333 $\pm$ 47	1909 $\pm$ 63	1976 $\pm$ 150		
Postburn	380 $\pm$ 42	385 $\pm$ 50	930 $\pm$ 219	526 $\pm$ 88		
Loss	1036 $\pm$ 43*	947 $\pm$ 56*	979 $\pm$ 159*	1450 $\pm$ 121*		
Nitrogen						
Preburn	9.3 $\pm$ 1.09	7.7 $\pm$ 0.43	14.1 $\pm$ 0.94	13.3 $\pm$ 1.81		
Postburn	1.6 $\pm$ 0.10	2.0 $\pm$ 0.16	4.9 $\pm$ 1.24	3.8 $\pm$ 0.68		
Loss	7.7 $\pm$ 1.00*	5.7 $\pm$ 0.40*	9.2 $\pm$ 1.08*	9.5 $\pm$ 1.45*		
Phosphorus						
Preburn	0.28 $\pm$ 0.021	0.25 $\pm$ 0.015	0.38 $\pm$ 0.012	0.38 $\pm$ 0.034		
Postburn	0.24 $\pm$ 0.018	0.22 $\pm$ 0.025	0.38 $\pm$ 0.051	0.40 $\pm$ 0.015		
Loss	0.04 $\pm$ 0.031	0.03 $\pm$ 0.025	0.002 $\pm$ 0.047	-0.02 $\pm$ 0.025		
Potassium						
Preburn	1.96 $\pm$ 0.134	1.70 $\pm$ 0.164	1.66 $\pm$ 0.113	1.47 $\pm$ 0.138		
Postburn	1.45 $\pm$ 0.201	1.39 $\pm$ 0.173	1.84 $\pm$ 0.336	1.43 $\pm$ 0.049		
Loss	0.51 $\pm$ 0.137*	0.31 $\pm$ 0.278	-0.17 $\pm$ 0.284	0.04 $\pm$ 0.102		
Calcium						
Preburn	11.9 $\pm$ 0.93	10.0 $\pm$ 0.27	25.1 $\pm$ 1.75	23.1 $\pm$ 2.74		
Postburn	11.8 $\pm$ 1.72	12.7 $\pm$ 1.68	22.2 $\pm$ 3.32	26.3 $\pm$ 2.25		
Loss	0.1 $\pm$ 1.43	-2.7 $\pm$ 1.86	2.9 $\pm$ 4.61	-3.2 $\pm$ 3.22		
Magnesium						
Preburn	1.63 $\pm$ 0.106	1.59 $\pm$ 0.041	2.24 $\pm$ 0.048	2.51 $\pm$ 0.096		
Postburn	1.53 $\pm$ 0.139	1.58 $\pm$ 0.167	2.22 $\pm$ 0.384	2.45 $\pm$ 0.141		
Loss	0.01 $\pm$ 0.111	0.01 $\pm$ 0.184	0.02 $\pm$ 0.411	0.06 $\pm$ 0.113		

from the ground and palm fronds pushed out from the stem apices. Hardwood recovery began somewhat later.

Essentially all the recovery during the first year was due to sprouting from belowground parts. Among the hardwoods only Dodonaea viscosa and Rhus copallina had any seedling regeneration, but this contributed an insignificant amount to the total recovery. The seedlings probably came from seeds present in the soil or litter before the burns; both genera are known to have fire-stimulated germination (Floyd 1966, Marks 1979). No data on reproductive activity were taken, but during the year following burning I observed flowering of every herbaceous species present in the plots. Within a month after the site 1 wet season burn Euellia carolinianensis was flowering and by 2 mo 15 additional species were in flower. Reproductive activity of palms was not noticeably different in burned and unburned areas. Most hardwoods did not flower during the first year after burning except for the weakly woody Lantana depressa, Morinda royoc, and Croton linearis. Occasional individuals of Psidium longipes, Brysonima lucida, Dodonaea viscosa, and Ficus citrifolia also flowered within the first year.

Herbs reached their preburn biomass levels within 7 mo following dry season burns and by 1 yr after wet season burns, even though the 2 mo recovery was greater after wet season burns (Fig. 11, Appendix B). In all four of the plots palm biomass by 7 mo was statistically

indistinguishable from preburn amounts. Hardwoods recovered more slowly than herbs and did not approach their preburn levels by the end of the first year. Recovery at 1 yr ranged from 18-39% of the preburn biomass. Certain hardwood species sprouted sooner than others (*D. viscosa* and *P. copallina* were two of the earliest). Hardwood biomass increased at each of the sampling periods following wet season burns, but showed no increase from 7-12 mo after the dry season burns (Fig. 11). The overall pattern of recovery indicates that April to August is a more favorable growing period than the rest of the year.

Before the fires, stems accounted for most of the hardwood biomass, whereas 1 yr after burning leaves accounted for equal or greater amounts than stems (Appendix B). Hardwood leaf biomass recovered to 32-68% of the preburn biomass but stems reached only 12-24% of the original amounts. The preburn stems, of course, represented the wood increments of 3.5-6.5 yr of growth.

The relatively rapid recovery of leaf biomass combined with complete recovery of herb and palm biomass means that the functional capacity for photosynthesis recovers faster than the structural characteristic of biomass. If one assumes that the sum of herb, palm, and hardwood leaf biomass is a measure of photosynthetic capacity, then the 1 yr recovery of the vegetation for wet and dry season burns is 82 and 93% at site 1 and 74 and 58% at site 2. The

corresponding recovery of total vegetation biomass (including hardwood stems) is 55, 63, 41, and 27%,

The aboveground net primary production of the understory for the first year after burning can be estimated by adding the litter produced during the year to the standing crop of biomass at the end of the year. There was no palm leaf litter and little hardwood leaf litter produced during the first year, and this litter was not measured separately from the hardwood litter resulting from the burns. There were substantial amounts of herb litter produced by 1 yr ( $11.7-39.5 \text{ g/m}^2$ , Appendix 8). Estimates of net production are 156 and  $166 \text{ g/m}^2\text{yr}^{-1}$  for wet and dry season burn plots at site 1 and 200 and  $144 \text{ g/m}^2\text{yr}^{-1}$  for wet and dry season burn plots at site 2. In addition to the few hardwood leaves shed by 1 yr and the loss of mass by herb litter through leaching and decomposition, herbivory is also not accounted for by this estimate. Grasshoppers and lepidopteran larvae were the most conspicuous invertebrate herbivores; the caterpillars of the echo moth (Seirarctia echo) grazed the young leaves of Zamia pumila very heavily. I also witnessed four white-tailed deer feeding on the young regrowth of one of the plots.

Because the herb and palm biomass 1 yr after burning were not significantly different from their preburn values, there is little evidence that the season of burning had an effect on their recovery. Variability in the data make it

impossible to detect small differences that might have a cumulative effect after several burns.

Hardwoods, on the other hand, showed marked differences in recovery among the four plots. The absolute recovery of hardwood biomass was greater at site 2, but that site had a much higher initial hardwood biomass. At site 1 the hardwood recovery was significantly lower following the wet season burn (29 g/m<sup>2</sup> or 20%) than the dry season burn (50 g/m<sup>2</sup> or 39%). At site 2 the trend was reversed, with greater recovery after the wet season burn (137 g/m<sup>2</sup> or 35%) than the dry season burn (78 g/m<sup>2</sup> or 18%). The most likely explanation for this apparent inconsistency is that fire temperatures had a greater effect on recovery than season of burn.

The recovery of nutrients in the understory vegetation followed a pattern very similar to that of biomass (Figs. 12-16, Appendix S). The main difference was the somewhat faster rate of recovery because of elevated nutrient concentrations in the young regrowth tissues. The recovery of Ca, however, was delayed somewhat relative to biomass because the 2 mo tissue concentrations of palms and hardwoods were lower than the preburn concentrations. Herbs in particular often reached preburn levels of nutrient standing crop earlier than biomass. For example, 2 standing crop in herbs was not significantly different from the preburn amount for both dry season burns at only 2 mo

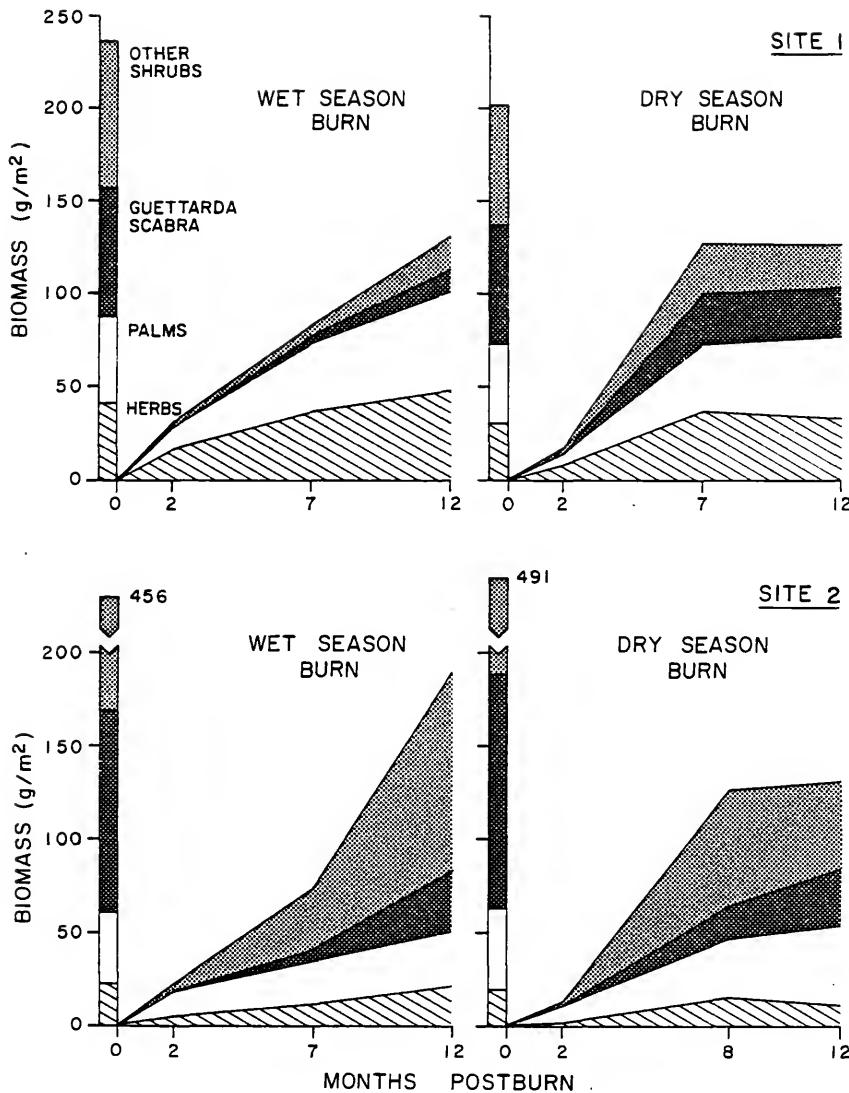


Figure 11. Postburn recovery of understory biomass. Bar on left shows preburn values.

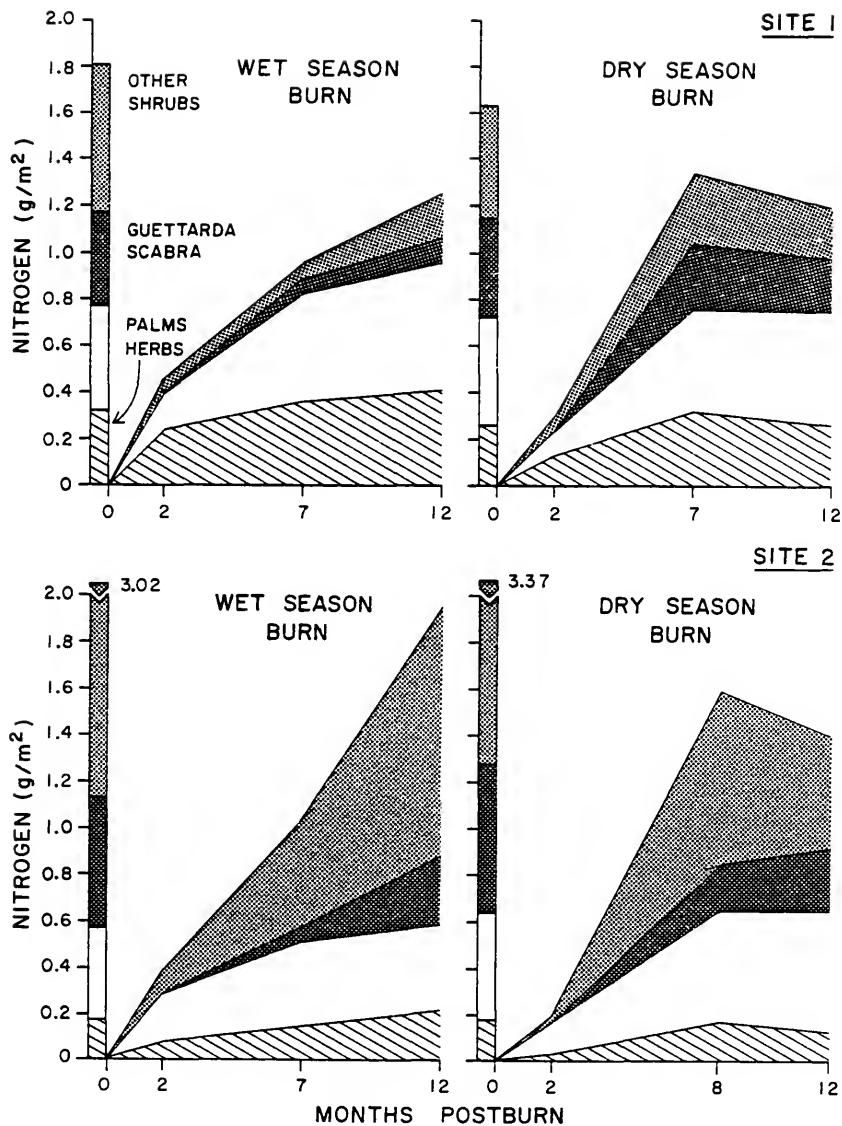


Figure 12. Postburn recovery of nitrogen in understory vegetation. Bar on left shows preburn values.

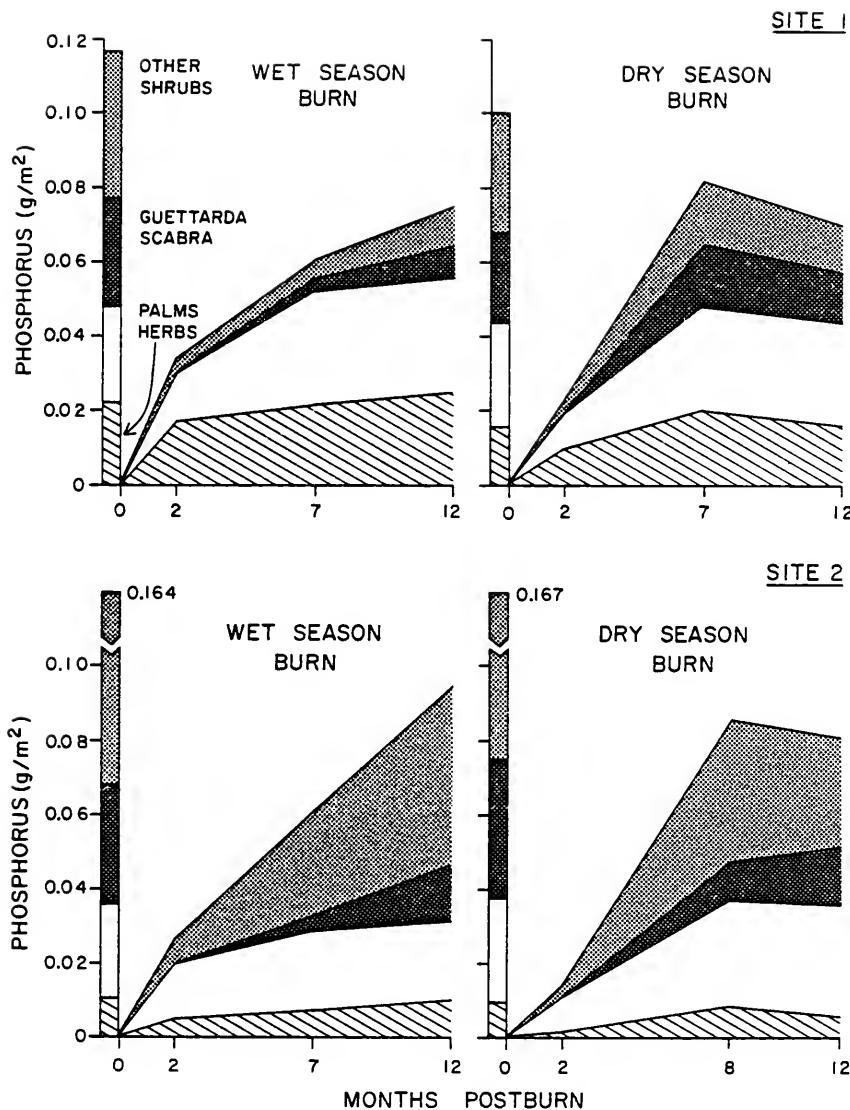


Figure 13. Postburn recovery of phosphorus in under-story vegetation. Bar on left shows preburn values.

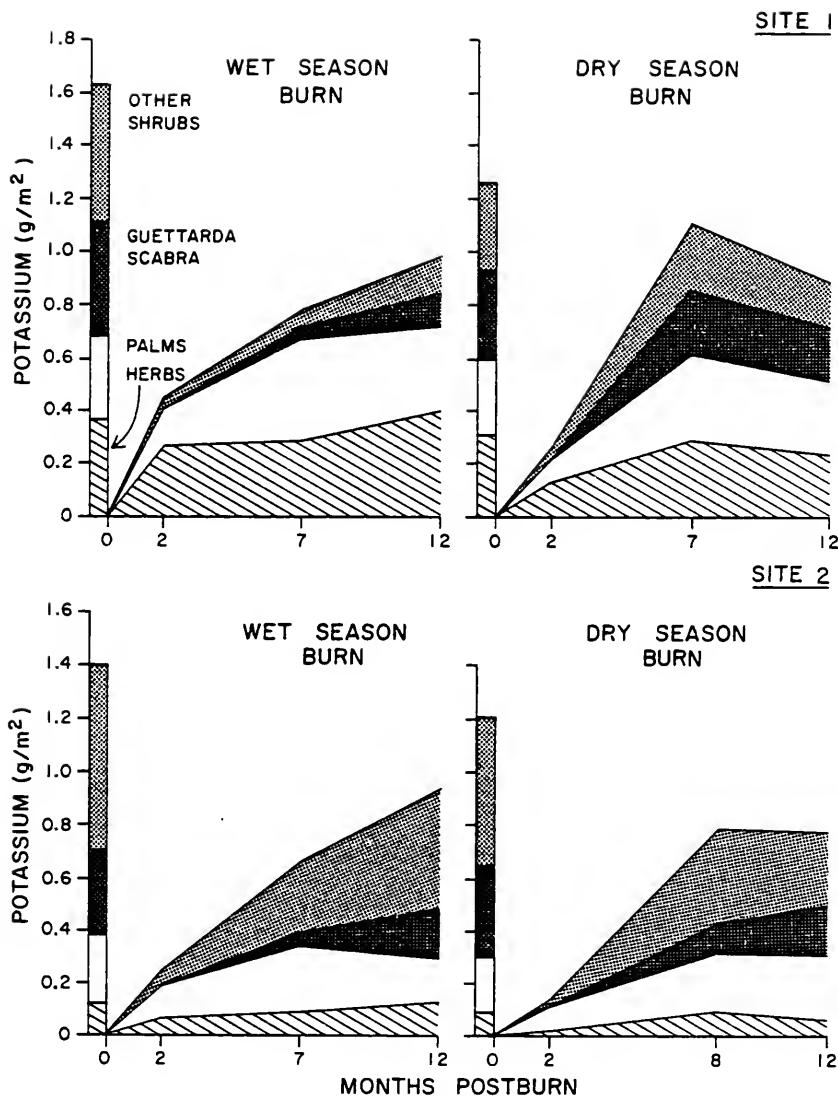


Figure 14. Postburn recovery of potassium in understory vegetation. Bar on left shows preburn values.

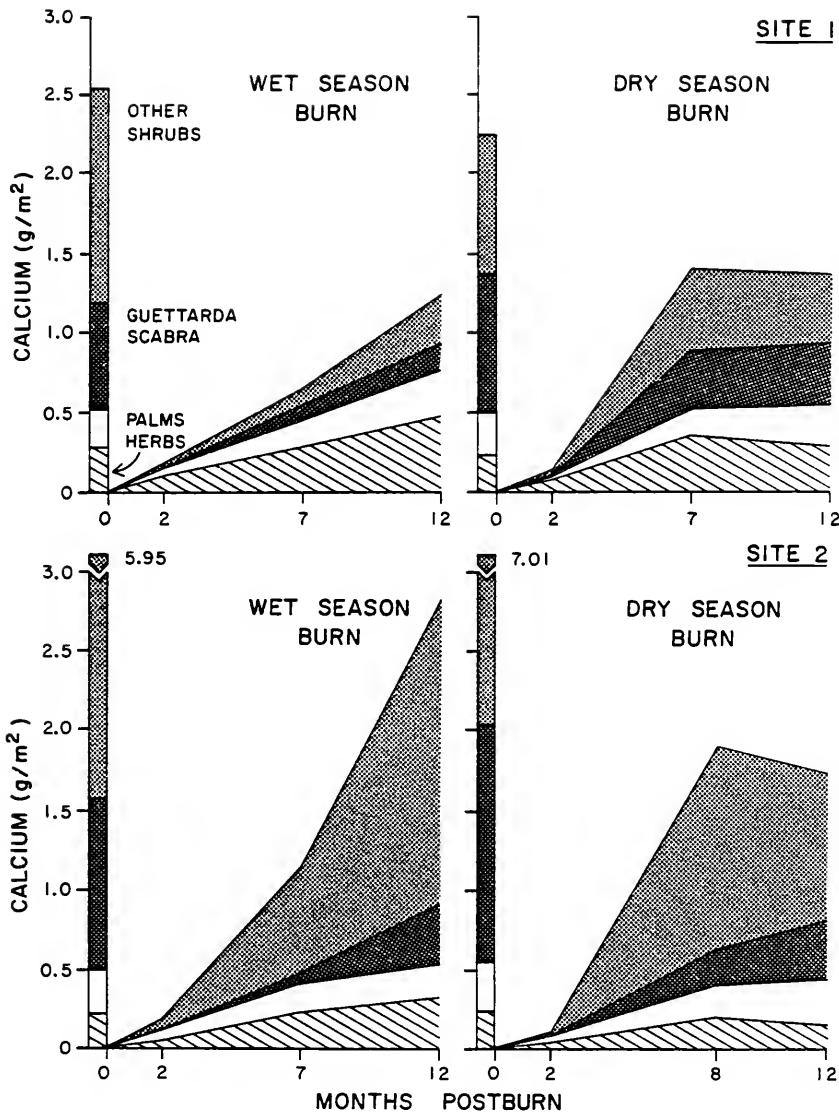


Figure 15. Postburn recovery of calcium in understory vegetation. Bar on left shows preburn values.

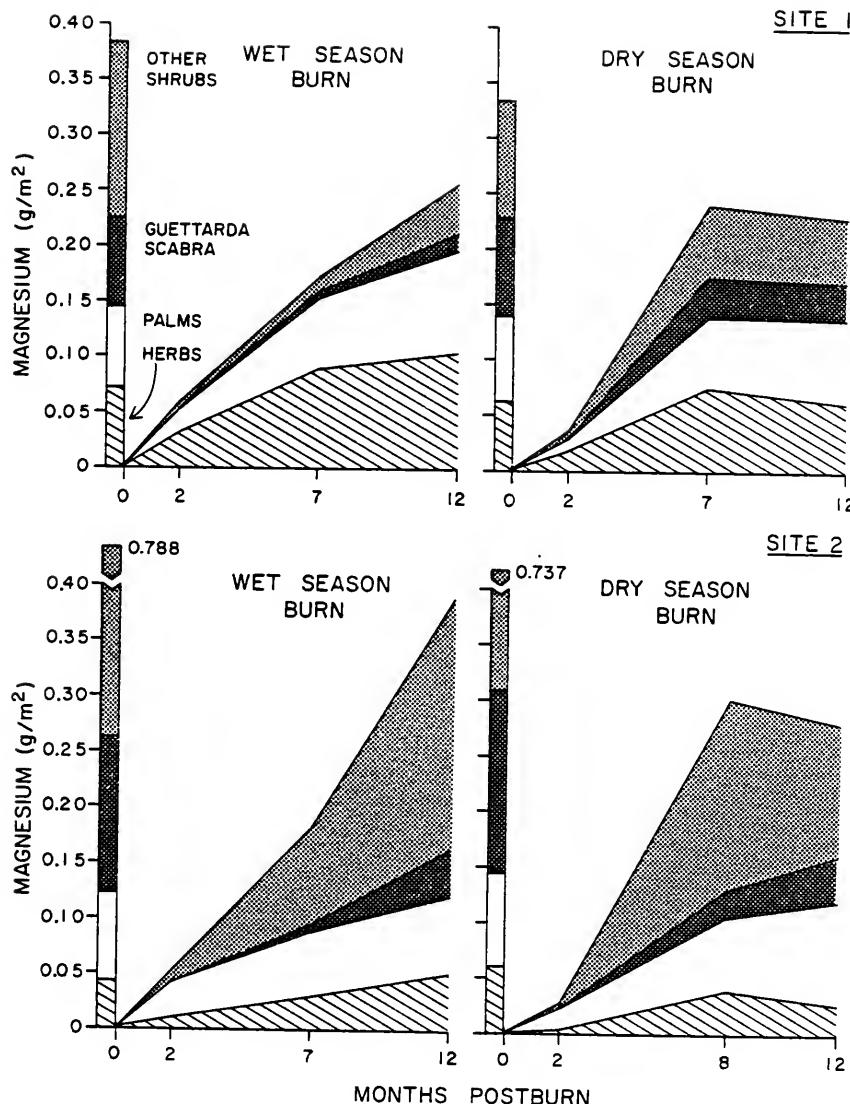


Figure 16. Postburn recovery of magnesium in understory vegetation. Bar on left shows preburn values.

postburn; the standing crop of K in herbs in the site 1 wet season plot also reached the preburn level by 2 mo. In one case (Ca, site 1 wet season burn) the standing crop was significantly higher 1 yr after burning than before the fire. For palms, both N and P standing crops were not significantly different from preburn at 2 mo for the site 2 wet season burn. All other palm nutrient standing crops, like palm biomass, did not reach initial amounts until 7 mo postburn.

The pattern of recovery of nutrient standing crops in hardwoods was the same as for biomass except that K at the site 1 dry season plot at 7 mo and the site 2 wet season plot at 12 mo were not different from the preburn amounts. The percent recovery of all nutrients in hardwoods at 1 yr was greater than the corresponding biomass recovery because of high nutrient concentrations. The percent recovery of the total vegetation nutrient standing crops was greater than the recovery of biomass for the same reason. The K standing crops in the two dry season plots at 1 yr were not significantly different from the preburn standing crops.

#### Litter

The standing crop of litter mass (and nutrients) during the 1 yr postburn period is a function of the amounts present immediately after the burns, inputs, and losses through leaching and decomposition. Even though nearly all

of the preburn understory litter was consumed in the burns (Figs. 9 and 10, Appendix B), the understory vegetation that was killed but not consumed by the fire replaced it. In the dry season plot in site 2 there was actually more after the burn than before. The understory litter compartment received no inputs for several months until herbaceous material began to die. By the 12 mo sampling period some of the hardwoods had also shed some leaves. At 1 yr some of the oldest palm fronds were becoming senescent, but were not dead and therefore not yet part of the understory litter.

There was some decrease in understory litter mass during the first two months after burning in all plots (Appendix B). From 2-7 mo after burning the dry season burn plots showed continued loss of mass (because these were wet season months), while the wet season plots did not (because it was dry). From 7-12 mo there was an increase in mass except at the site 2 dry season plot where decomposition outpaced meager litter production by shrubs and herbs. At site 1 much of the input to understory litter is attributable to herbs.

At the end of the first year the standing crops of understory litter mass were not different from amounts present immediately after the burns, except for the site 2 dry season plot. However, the standing crops were below their preburn levels except at the site 2 wet season plot where there was a large amount of unconsumed vegetation and rapid recovery of litter-producing hardwoods.

The standing crops of nutrients in the understory litter showed various patterns during the postburn year. Large decreases often occurred during the first postburn rainy period, 0-2 mo following wet season burns and 2-7 mo after dry season burns. Potassium in particular showed leaching losses of >80-90% of the amount in the postburn litter. For most of the nutrients there was some net increase during the 7-12 mo period. Phosphorus, however, showed initial losses and no significant change during the last 5 mo period. Nitrogen and Ca showed the least net loss during the year and were not different from the amounts present immediately after the burns (except for the site 2 dry season plot which lost mass throughout the period).

In contrast to the understory litter compartment, which had no inputs during the first several months after burning, the pine litter received continual inputs. Pine needles fall throughout the year, but at highest rates during the wet season (Fig. 17). Short term peaks in needlefall are caused by high winds. The annual needlefall was about 320 g/m<sup>2</sup> for site 1 and 260 g/m<sup>2</sup> for site 2 (Table 9). Needlefall constitutes 75-80% of total pine litterfall. Pine branches, mostly <3 cm diameter, contribute about a tenth of the litterfall mass, and seed cones and miscellaneous materials make up about the same fraction. Some year-to-year variation in litterfall is to be expected; needlefall during the study period was about average at

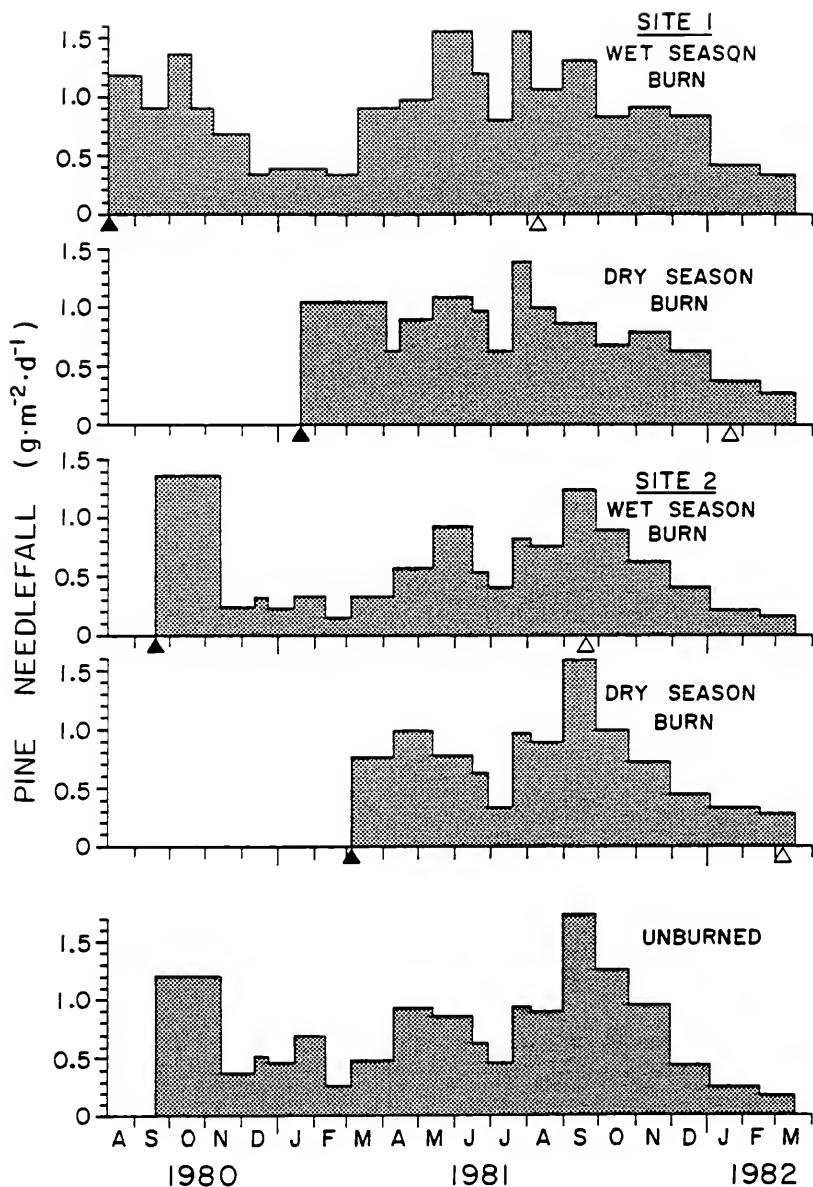


Figure 17. Pine needlefall in the study plots and an unburned area of site 2. Closed triangles show time of burn and open triangles the 1 yr anniversary of the burn. Absence of bars means that no sampling was done.

Table 9. Annual pine litterfall summary. Miscellaneous fraction includes bark and pollen cones. Standard errors for dry mass based on n = 4 for needles and misc., n = 14 for branches and cones.

Plot	Litter fraction	Dry mass (g/m <sup>2</sup> )	(mg/m <sup>2</sup> )			
			N	P	K	Ca
Site 1 wet season burn						
Needles	326.5±14.8	1043	45.7	126.0	1514	510
Misc.	42.4±5.59	142	6.6	6.9	157	18
Total <sup>a</sup>	443.5	1362	58.8	161.1	1949	561
Site 1 dry season burn						
Needles	319.0±22.0	1019	44.7	123.1	1480	498
Misc.	29.8±1.14	97	3.9	8.7	113	17
Branches	41.6±4.3	114	3.7	5.8	260	15
Cones	23.0±2.78	63	2.8	22.4	18	18
Total	413.4	1293	55.1	160.0	1871	548
Site 2 wet season burn						
Needles	240.5±13.4	772	29.1	59.4	1299	387
Misc.	23.9±0.84	75	2.6	2.8	142	9
Total	305.0	959	35.9	71.7	1668	413
Site 2 dry season burn						
Needles	277.0±11.6	889	33.5	68.4	1496	445
Misc.	25.5±0.83	95	3.0	5.1	171	15
Branches	36.0±3.0	99	3.6	5.0	223	13
Cones	4.6±0.60	13	0.6	4.5	4	4
Total	343.1	1096	40.7	83.0	1894	477
Site 2 unburned						
Needles	282.0±17.0	905	34.1	69.7	1523	453
Misc.	17.5±0.84	62	2.2	2.9	86	9
Total <sup>a</sup>	340.1	1079	40.5	82.1	1836	479

<sup>a</sup> Assumes same branch and cone deposition as dry season burn plot at the same site.

other locations in Long Pine Key (A. Herndon, unpublished data). The number of seed cones was probably higher than average, at least for site 1, because there was a better than average seed crop in the autumn of 1980. The deposition of nutrients through pine litterfall ranged from about 2 g/m<sup>2</sup> of Ca and 1 g/m<sup>2</sup> of N to 0.03-0.05 g/m<sup>2</sup> of P (Table 9). One notable aspect of the nutrient inputs is the high concentration of K and the low concentration of Ca in pine cones relative to other litter types.

Pine litter makes up the major portion of the fuel mass. The material remaining after a fire is mostly heavier pieces such as branches and cones, unless the fuel is moist (e.g. site 2 wet season burn). Pine litter mass showed a more or less continuous increase except for the 0-2 mo period following the wet season burns where moist conditions and the nutrients released in the ash may have stimulated decomposition. By 1 yr all plots were still far below preburn levels: site 1 about 50% and site 2 33-40% of preburn.

The nutrient standing crops in pine litter showed a pattern very similar to mass with some decrease 0-2 mo following wet season burns and increases otherwise. The percent recovery at 1 yr was similar to mass for all nutrients except N, which only reached about 33% at site 1 and 20% at site 2.

The recovery of total litter mass followed a pattern dominated by the pine litter except for the decline between 7 and 12 mo at the site 2 dry season burn plot caused by a drop in understory litter. At one year litter mass was 42-62% of its preburn level. Phosphorus and Ca recovered in proportion to dry mass. Nitrogen was much lower than dry mass (26-37%) because C:N ratios decrease with decomposition. Potassium recovery was high relative to mass, especially at site 2, because of the high proportion of relatively unweathered litter materials.

#### Impact of Fires on Pines

There is some indication of a slight increase in the rate of needlefall immediately following the burns (Fig. 17), even though there was little scorching of needles. The stress of high temperatures may lead to senescence of needle fascicles earlier than normal.

In both site 1 plots there was no mortality of pine trees during the year after burning (Fig. 5). In contrast, at site 2, where the trees were smaller, some trees died (Figs. 6 and 7). In the wet season plot at site 2 six trees were dead 1 yr after the burn and in the dry season plot 98 trees were dead, including virtually all trees < 7 cm dbh. None of these trees showed substantial scorching and all appeared to be healthy for the first few months after the fires. There was evidence of bark beetle activity in all the dead

trees, but there is no way of knowing whether the insects were responsible for the deaths of the trees or whether they only attacked trees that were already dying. It is clear, however, that high temperatures around the stems of South Florida slash pine trees can lead to their deaths. Three years after the dry season burn at site 2 most of the pines had cracks exuding resin in the bark of the basal 1-2 m of the trunk.

Under the burning conditions of the experimental burns all pine seedlings were killed by the fires (Table 10). The season of burning has a pronounced effect on the establishment of new seedlings. Seedfall is from September into November; therefore burns that occur in the wet season before seedfall create excellent conditions for seed germination and seedling establishment. Burns that occur in the dry season (after seedfall) destroy the current year's seed crop and by the next period of seedfall conditions are less favorable for seedling establishment. The 1980 seed crop in Long Pine Key was relatively good and the wet season burn plots had much higher seedling densities 1 yr later than did plots burned in the dry season (Table 10).

Table 10. Density of pine seedlings (no./m<sup>2</sup>, expressed as mean  $\pm$  standard error) in the study plots. Each mean based on 24, 1 x 1 m quadrats except for the preburn samples at site 2 where n = 12.

Site	Plot (Burn season)	Preburn	Months postburn			
			0	2	7	12
1	Wet	1.17 $\pm$ 0.32	0	8.67 $\pm$ 1.21	8.88 $\pm$ 1.38	6.79 $\pm$ 0.99
	Dry	1.46 $\pm$ 0.37	0	0.08 $\pm$ 0.084	0	0.29 $\pm$ 0.112
2	Wet	0.33 $\pm$ 0.189	0	2.71 $\pm$ 0.61	1.83 $\pm$ 0.31	1.96 $\pm$ 0.38
	Dry	0.08 $\pm$ 0.084	0	0.13 $\pm$ 0.125	0.04 $\pm$ 0.041	0

### Soil

Soil analyses show some striking differences in the properties of the substrate between the two sites (Table 11). These differences are largely due to the presence of pockets of the reddish-brown "Redland" soil at site 1. The wet season plot had 8.2% (S.E.=1.62) of the surface covered by mineral soils and the dry season plot 8.4% (S.E.=1.42). A very few pockets of the Redland soil were present in the site 2 dry season plot and none were seen in the site 2 wet season plot.

The organic matter content of the soils was much higher at site 2 (about 46%) than site 1 (about 18%), although both sites are relatively high for upland soils. The higher organic content may account for the slightly lower preburn pH at site 2. Preburn extractable K and Mg do not show much difference between sites, although K may be somewhat higher at site 2. Phosphorus is much higher at site 2 than site 1, suggesting a relationship with organic matter.

Burn effects on soil properties remaining 1 yr postburn include an increase in pH. This was most pronounced in the site 2 samples and in the paired Redland soil samples taken in site 1, where initial pH was lower. Soil organic matter was unaffected by burning. There is an indication that extractable P was reduced 1 yr after burning. The amounts extractable by weak acid in the Redland soil samples were below detection limits both in burned and unburned soil.

Table 11. Results of soil analyses of soil samples collected from throughout the plots and samples restricted to the patches of Redland mineral soil (means  $\pm$  standard errors,  $n = 12$ ). Significant differences shown by one ( $p = .05$ ) or two ( $p = .01$ ) asterisks.

Site	Plot (Burn season)	Time of sampling	pH	Organic matter (%)	P			K			Mg		
					(mg/kg)			(mg/kg)			(mg/kg)		
1	Wet	Preburn	7.27 $\pm$ .087	17.9 $\pm$ 0.99	0.21 $\pm$ .051	41.3 $\pm$ 2.32	16.2 $\pm$ 4.4						
Dry		Preburn	7.19 $\pm$ .065	18.2 $\pm$ 1.21	0.26 $\pm$ .089	35.3 $\pm$ 1.39	16.9 $\pm$ 5.5						
		1 yr postburn	7.28 $\pm$ .076	19.6 $\pm$ 0.76	0	39.7 $\pm$ 1.68	19.1 $\pm$ 7.5						
2	Wet	Preburn	7.00 $\pm$ .081	45.4 $\pm$ 3.91	1.48 $\pm$ .458	55.7 $\pm$ 5.02	16.7 $\pm$ 17.8						
Dry		Preburn	6.86 $\pm$ .084 **	47.5 $\pm$ 3.73	1.42 $\pm$ .158	49.0 $\pm$ 3.60	21.6 $\pm$ 11.4						
		1 yr postburn	7.37 $\pm$ .067	46.6 $\pm$ 3.85	1.14 $\pm$ .171	39.3 $\pm$ 1.71	24.3 $\pm$ 9.8						
<u>Redland Soil</u>													
1	Unburned	Same as below	6.06 $\pm$ .054	8.2 $\pm$ 0.39	0	26.2 $\pm$ 1.06	20.0 $\pm$ 10.7						
Dry		1 yr postburn	6.40 $\pm$ .070	9.2 $\pm$ 0.67	0	35.3 $\pm$ 1.19	19.1 $\pm$ 5.8						

Extractable Mg may be somewhat higher after burning, at least at site 1. Burning increased extractable K in both types of soil samples at site 1 but the increase was statistically significant only for the Redland soil. At site 2 there was a decrease in K after burning. This may result from more rapid uptake by the vegetation at site 2.

## CHAPTER IV DISCUSSION

### Fire-caused Losses of Nutrients

One of the most obvious effects of fire is the removal of organic matter. Nutrients are also lost by volatilization or particulate emissions. Numerous studies have attempted to measure these losses in several kinds of ecosystems. In prescribed burning situations it is possible to sample standing crops before and after the fire, as was done in this study. With wildfires the approach has usually been to compare standing crops in the burned area with nearby unburned analogs (e.g. Grier 1975). Spatial heterogeneity of fuels and the collecting of postburn ash pose problems for field studies (Paison 1980). For example, in a light prescribed burn in southeastern coastal plain pine forest, Binstock (1978) and Nguyen (1978) measured higher mean values of mass and nutrients after the burn than before. In a study of fire in heather ecosystems in England Evans and Allen (1971) gave up on field measurements and performed artificial burns in the laboratory. This represents the other common approach to measuring losses during fires. Simulated burning has been done both as open ignition or in a muffle furnace. The additional accuracy in measuring

losses, however, is at the expense of the realism of the burning conditions.

Table 12 presents the average mass balance for the four burns in this study along with data from several other southeastern pinelands and a few other ecosystems. The table does not include examples of slash burning (e.g. Harwood and Jackson 1975, Ewel et al. 1981). Comparisons must be tempered with a degree of caution because methodologies and conventions differ somewhat among the studies. In some cases the fuel represents only the forest floor (litter) and in others litter and vegetation. The studies by Hough (1981), Kodama and Van Lear (1990), Richter et al. (1982), Debano and Conrad (1978), and Grier (1975) involved field sampling of ash. Debano and Conrad vacuumed the litter and ash in their study of chaparral. Hough picked up the ash "by hand" and stated that some ash was not collected. The study by Hough (1981) deals with the situation most similar to the Miami Rock Ridge pinelands. The overstory was mixed stands of slash and longleaf pines with relatively dense understories dominated by Serenia glauca (saw palmetto) and Ilex glabra (gallberry).

The fuel consumption in the Long Pine Key burns was within the range of the other pineland burns (Table 12). The lower consumption (both absolute and percentage) in three of the other southeastern pineland burns is due to high moisture content of the lower layers of the forest

Table 12. Losses of mass and nutrients during fires in southeastern pine forests and other ecosystems. Under fuel type L = litter and V = vegetation not including trees.

Ecosystem and Reference	Fuel type	Dry mass		N g/m <sup>2</sup>	% initial amount
		g/m <sup>2</sup>	% initial amount		
This study (mean of all burns)	L+V	1103	6.7	8.0	72
Slash Pine-Palmetto-gallberry, Georgia and Florida (Hough 1981)	L+V	651	[ ]	2.8	58
"	L+V	740	[ 40- 74 ]	4.3	66
"	L+V	1869	[ ]	11.2	41
"	L+V	2538	[ ]	19.4	64
Loblolly Pine Plantation, South Carolina (Koedam and Van Lear 1980)	L	685	19	4.5	13
Loblolly Pine, South Carolina (Wells 1971)	L	730	27	11.2	33
Loblolly Pine, South Carolina (Richter et al. 1982)	L	500	23	2.4	14
Wiregrass-Longleaf Pine, North Carolina <sup>a</sup> (Christensen 1977)	L+V	670	84	2.2	66
Limestone Grassland, England <sup>a</sup> (Lloyd 1971)	L+V	174	87	1.3	73
Heathland, England ab (Evans and Allard 1971)	V	--	47-61	--	43-57
Heathland, England <sup>a</sup> (Allen 1964)	V	--	62-76	--	68-76
Chaparral, California (DeBano and Conrad 1978)	L+V	2445	61	11.0	39
Conifer forest, Washington (Entiat wildfire) (Grier 1975)	L	6770	96	81.7	97

<sup>a</sup> Simulated burn.

<sup>b</sup> Outdoor burning of 3-6 kg samples of Calluna vulgaris shoots.

<sup>c</sup> Laboratory burning of 50 g samples of chopped Calluna vulgaris shoots.

Table 12. continued

Ecosystem and Reference	P		K		Ca		Mg	
	% initial amount		g/m <sup>2</sup> % initial amount		g/m <sup>2</sup> % initial amount		g/m <sup>2</sup> % initial amount	
	g/m <sup>2</sup>	% initial amount	g/m <sup>2</sup>	% initial amount	g/m <sup>2</sup>	% initial amount	g/m <sup>2</sup>	% initial amount
This study (mean of all burns)	0.01	4	0.17	10	-0.7	-4	-0.05	2
Slash Pine-Palmetto-gallberry, Georgia and Florida (Hough 1981)	0.15	26	0.90	61	1.3	37	0.18	22
"	0.25	47	0.90	63	2.5	63	0.46	58
"	0.46	23	1.06	23	2.3	25	0.77	32
"	0.84	44	2.45	51	5.0	46	1.24	47
Loblolly Pine plantation, South Carolina (Wodrama and Van Lear 1980)	0.21	8	1.20	20	1.2	9	0.91	22
Loblolly Pine, South Carolina (Wells 1971)	--	--	--	--	--	--	--	--
Loblolly Pine, South Carolina (Richter et al. 1982)	--	--	--	--	--	--	--	--
Wiregrass-Longleaf pine, North Carolina <sup>a</sup> (Christensen 1977)	0.16	47	0.42	40	0.4	20	0.04	11
Limestone grassland, England <sup>a</sup> (Lloyd 1971)	0.03	25	0.26	39	0.1	9	--	--
Heathland, England <sup>ab</sup> (Evans and Allen 1971)	--	5-14	--	7-20	--	7-12	--	3-14
Heathland, England <sup>ac</sup> (Allen 1964)	--	0.6-3.5	--	1.4-4.9	--	0.1-2.4	--	0.4-2.1
Chaparral, California (DeBano and Conrad 1978)	0.02	0.6	4.59	16	1.1	2	-4.72	-25
Coniferous forest, Washington (Grier 1975)	--	--	27.0	79	7.6	19	2.4	31

floor (Sweeney and Biswell 1961). Wildfires under extreme conditions can of course lead to very large losses (Grier 1975). Grassland fuels (Lloyd 1971, Christensen 1977) also have high percentage consumption rates.

The losses of N seem, for all practical purposes, to be proportional to losses of total mass. Hough (1981) developed a regression equation to describe the loss of N in prescribed burns:

$$N \text{ (kg/ha)} = -10.55 + 0.0071(X)$$

where X is the loss of mass in kg/ha. The mean N concentration in the fuel of these stands is about 0.75% (Hough 1982). In a field study not included in Table 12, Klemmedson et al. (1963) found losses of 30% of mass and 31% of N after prescribed burning of ponderosa pine litter. In a lab study Knight (1966) burned conifer forest floor samples in a muffle furnace and found losses of 39 and 25% for mass and N, respectively, at 300°C and 63 and 64% at 600°C. In lab studies on southeastern pine litter in which fuel samples were simply ignited, DeBell and Ralston (1970) recorded losses of 71% of the mass and 58% of N while Lewis (1975) found losses of 39 and 56% for mass and N, respectively. In these relatively cool burns most of the N was lost as dinitrogen gas.

Fires may also result in losses of the so-called ash elements (Clayton 1975, Table 12). However, under most

circumstances it is not possible to show statistically significant losses by preburn and postburn sampling (e.g., this study and Richter et al. 1982). The magnitude of these losses as presented in much of the literature is likely to be overestimated. In field studies it is difficult to sample the ash. When small plots are burned, and especially if samples of fuel are burned in laboratory settings, there is no opportunity for the particulate matter to settle back down on the sampled area. Significant amounts of nutrients in particulate matter are carried away from small burns (Smith and Bowes 1974, Evans and Allen 1971). In more extensive burns much of the particulate fraction of smoke will return directly to the ground. Some of the particulate emissions are deposited on the canopy and are returned to the forest floor by the first rain after the burn. There is also a tendency to consider any loss reported in the literature as real while gains after burning are ignored (e.g. Boerner 1982). For example, the increase of 25% in the amount of Mg reported by Debano and Conral (1978, Table 12) makes the loss of 16% of K seem of questionable significance.

The ash element most likely to be lost by volatilization is K, which is volatilized at temperatures above 500°C. In what are probably the two hottest fires listed in Table 12 (chaparral and the Entiat wildfire) the percentage of K lost was higher than that of any other ash element. This was also true of the lab simulations on heather.

The ash deposited on the soil surface is subject to erosion losses on sloped terrain, but not in South Florida. Much of the mineral content of the ash is easily leached into the soil by rainfall (Allen 1964, Lewis 1974, Christensen 1977). Recently burned ecosystems may experience losses to groundwater, however these losses seem to be very small for coastal plain pinelands (Boerner and Forman 1982, Richter et al. 1982). In Long Pine Key the high soil organic matter content should give the soil a high cation exchange capacity and P should be quickly immobilized by the abundant Ca. The rapid recovery of the vegetation also acts as a sink for the nutrients released by the fire (see below).

Although the losses of nutrients (other than N) in the burns in this study were not statistically significant it is certain that some losses did occur. However, even if one assumes a loss of 10% of the standing crop of the ash elements, these losses could be replaced by precipitation inputs over the period of a burning rotation, 3.5-6 yr. Annual deposition of N, P, K, Ca, and Mg in bulk precipitation in northcentral Florida is about 1-1.4, 0.1, 0.3-0.6, 1-1.5, and 0.2 g/m<sup>2</sup> respectively (Hendry and Brezonik 1980, Riekerk et al. 1979). Depending upon the estimate of N input by precipitation, this may or may not replace the substantial loss of N because losses ranged from 1.4-2.2 g\*m<sup>-2</sup>\*yr<sup>-1</sup> when averaged over the time since the previous fire.

It is to be expected that nutrient losses should more or less equal inputs in ecosystems that have a long history of frequent burning. In fact, fire may be a mechanism by which nutrient-poor ecosystems prevent the accumulation of nutrient capital.

Several agents of biological N-fixation could aid in recovery of N lost through burning. Although several herbaceous legumes are common (e.g. *Cassia* spp., *Crotalaria pumila*) they are not likely to fix significant amounts (Bundel 1981). *Lysiloma latisiliqua* is a leguminous tree, but it is not common enough in pinelands to add much nitrogen. *Zamia pumila* has a blue-green algal endophyte that fixes N (Lindblad 1984). *Myrica cerifera*, an actinomycete-nodulated shrub, has substantial biomass in much of Long Pine Key (including site 2) and may fix appreciable amounts of N. In a northern Florida slash pine plantation Permar and Fisher (1983) estimated that *M. cerifera* with a crown cover of 8% fixed  $1.1 \text{ g N*m}^{-2}\text{*yr}^{-1}$ .

Nonsymbiotic N fixation by soil microorganisms in forest ecosystems has often proved to be a rather minor source of N relative to precipitation inputs (Ijepkema 1979). Jorgensen and Wells (1971) found indications of increased soil acetylene reduction activity in burned loblolly pine plots compared to unburned controls. A later study by Jorgensen (1975) did not support this finding and found N-fixation rates of  $< 0.1 \text{ g*m}^{-2}\text{*yr}^{-1}$ . Vance et al. (1983) found even

lower rates ( $0.01 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) and no effect of long-term prescribed burning in oak-hickory forest. In a prairie site, DuBois and Kapustka (1983) measured  $0.8 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  of nonsymbiotic N-fixation, about half of which was due to cyanobacteria. Blue-green algae are not found in acid coastal plain soils (Jurgensen and Davey 1968) but they are common in circumneutral soils (Granhall and Henriksson 1969) and abound on the oolitic limestone of the Miami Rock Ridge. I ran an acetylene reduction assay on a few samples of rock from the study area and found measureable rates after 24 hr of incubation. Crude calculations indicated rates on the order of  $0.1 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ . It would seem that fixation by various taxa plus precipitation inputs over a burning rotation could easily account for the losses of N recorded for the experimental fires.

#### Postfire Recovery

In the Miami Rock Ridge pinelands virtually all recovery of understory species is by vegetative means rather than by seedling reproduction. This is fairly common in ecosystems that experience high fire frequencies. Abrahamson (1984a) found very little change in species composition after fires in several pine-dominated plant communities in southcentral Florida. Boerner (1981) also noted relatively little change in species composition in burned areas of the New Jersey Pine Barrens.

This is in contrast to situations, often where fires are of lower frequency but higher intensity, in which there is a distinctive postburn flora. The large number of herbaceous annuals that appear after chaparral fires is a dramatic example (Christensen and Muller 1975). The degree to which species changes result from burning depends in part on the severity of the fire. In jack pine communities, fires during the dry summer months consume the upper organic layers of the soil, whereas fires during the moister spring do not. Since species with shallow regenerative organs are eliminated by ground fires, numerous postfire disturbance species like Epilobium (fireweed) become established after summer fires (Ohmann and Grigal 1981).

Even though recovery in the rock ridge pinelands is vegetative, there are differences among the different growth forms in the rate of recovery. Herbs and palms regrow very quickly, reaching their preburn dry masses within 1 yr. The monocots (graminoid herbs and palms) and ferns have protected meristems that are seldom damaged by fires. Grasses are well known for their rapid regrowth after top removal (Wilson and Lewis 1962, Daubenmire 1968). The recovery of dicots (whose buds are usually killed) requires the activation of previously inactive meristems or the production of adventitious buds, whether they be on rhizomes, roots, or the base of stems; woody dicots take longer than herbaceous dicots to show regrowth. However, a

study by Hough (1965) in Georgia found that Serenoa repens only reached 55% of its preburn mass 1 yr after burning whereas Ilex glabra, a hardwood, returned to 70% of its preburn level. This is somewhat anomalous because the preburn vegetation had been unburned for 15 yr and there should have been considerable stem biomass. S. repens was found to have greater cover 1 yr after a burn than before the burn in a study by Abrahamson (1984b). This agrees more closely with my findings in the rock ridge pinelands.

By 1 yr after the experimental burns, 130-190 g/m<sup>2</sup> of regrowth vegetation appeared in the burned plots. This is a fairly large amount in relation to some other postburn recoveries. One year after a prescribed burn in the New Jersey Pine Barrens the regrowth of herbs, shrubs, and oak sprouts was 113 g/m<sup>2</sup> (Boerner 1981). In jack pine stands burned by wildfires in Minnesota the vegetation recovery ranged from 21-101 g/m<sup>2</sup> after one complete growing season (Ohmann and Grigal 1981).

The recovery of photosynthetic capacity is even more rapid than the recovery of biomass because hardwoods produce leaves more rapidly than support tissues. In the four burns in Long Pine Key the recovery of photosynthetic tissues (sum of herbs, palms, and hardwood leaves) was 58-93% of the preburn amount at the end of 1 yr. The first year recovery of hardwood leaves alone ranged from 32-68% of the initial quantities. The rapid recovery of photosynthetic surface is

also found after fires in other South Florida slash pine ecosystems. Sandy flatwoods with an understory of grasses, *S. repens*, *I. glabra*, and several ericaceous species regained from 57-83% of their original cover within a year after burning (Abrahamson 1984a).

#### Effect of Season of Burning on Hardwood Recovery

Several studies in southern U. S. pinelands have shown that prescribed burning during the growing season kills back a greater percentage of hardwood stems and larger hardwood stems than dormant-season fires (Chaiken 1952; Ferguson 1957, 1961; Lotti et al. 1960; Brendler and Cooper 1968; Langdon 1981). In the present study all understory hardwood stems were killed by the fires regardless of season. This is because there were no stems with basal diameters > 7 cm and the burns were very even and complete. Of greater interest, therefore, is the relative recovery of these hardwoods (by sprouting) following burns at different seasons.

The pattern of sprout recovery after burns at different seasons parallels, in general, that of topkilling: greater recovery after winter burns than summer burns. Ferguson (1961) in east Texas found, however, that although summer (August) burns killed back more hardwood stems than winter (December) burns, the sprouts resulting from these burns were larger and more numerous than those produced by late

winter (February-late March) or spring (late April-May) burns.

Different measures of recovery have been used in different studies. The data most commonly reported are density of stems (sprouts) and cover, with sprout height occasionally given. Only rarely is biomass (as used in this study) or some measure of volume used. Density alone can be a misleading measure because topkilled hardwoods usually produce several sprouts, and therefore burning appears to increase hardwood density, but not necessarily biomass or total leaf area.

Results of a long-term study of prescribed burning in South Carolina coastal plain loblolly pine stands have been reported after 10 (Lotti et al. 1960), 20 (Lewis and Harshbarger 1976), and 30 yr (Langdon 1981) of treatments. The burning treatments, begun in 1946 and 1951, include annual burns and periodic burns (> 3 yr interval) in both summer and winter and biennial summer burns. Summer burns are conducted as soon after June 1 as conditions permit and the winter burns after December 1. Interpretation of the results is not entirely straightforward because the treatments were sampled at different postburn ages. However, it is clear that summer burns result in reduced hardwood cover relative to winter burns done at the same frequency. The reduction is due to a combination of increased mortality and less vigorous regrowth. In fact,

biennial summer burning is more effective than annual winter burning at reducing the number of stems and crown cover of woody undergrowth when the longer recovery period is accounted for. The annual summer treatment virtually eliminated woody plants < 12.5 cm dbh. It is unlikely that the Long Pine Key pinelands could burn more frequently than once every 2 yr, even on the most productive sites. The periodic summer burning in the South Carolina study reduced the cover of woody plants relative to winter burning in spite of producing a greater number of stems (Langdon 1981).

In Louisiana Grelen (1975) found that plots that had been burned by six biennial July burns had less cover of hardwoods (including *Myrica carifera* and *Phus copallina*) than plots burned in March or May. Hodgkins (1958) in Alabama found a greater recovery of shrubs and vines after a single January burn than a single August burn. Hughes and Knox (1964) followed the recovery of *Ilex glabra* after a series of three annual burns conducted in January, April, June, August, and October. They reported sprout density, height, and cover. Even after three burns all treatments showed an increase in number of stems relative to the initial number. All burning treatments also resulted in a decrease in average stem heights. Cover, which may be the best single measure of the three measures they reported for assessing recovery, was decreased for all months except April. June and August burns gave the greatest decreases in

cover and August and October burn plots had the shortest sprouts. Based on the available data it would appear that the recovery of biomass was least after the August burns, followed by June and October.

There are two frequently suggested explanations for this seasonal effect of fires, which can be described as the physical and the physiological. The physical explanation is based on the fact that summer fires are "hotter", because of higher ambient temperatures and often drier fuel conditions. The higher ambient temperatures mean that the vegetation itself is warmer and, therefore, that less heat is required to raise the tissue to a lethal temperature (Pyram 1948, Hare 1961). Hare (1965a) demonstrated that it took about 50% longer for a torch flame applied to a longleaf pine trunk to raise the temperature of the cambium to 60°C when the initial temperature was near 0 instead of 16°C. This argument is mostly applied to topkilling of stems but it can be applied equally well to the degree of damage to the rootstock. A fire when the initial temperature of the soil and rootstock is high should kill more tissue so that less nutrient reserves and fewer buds are available for recovery.

In subtropical South Florida pinelands the temperature difference between summer and winter is less than that found at higher latitudes. Lotti et al. (1960) reported ambient temperature differences of about 14.5°C in South Carolina. Summer and winter burning conditions in east Texas differed

by about 19°C (Ferguson 1961). The differences for the two pairs of burns in rock ridge pineland were 11.5 and 8°C.

The other explanation is that the plants in question are physiologically more susceptible to heat injury and less able to recover by sprouting a certain times of the year (Hare 1961). These times of year are of course related to the phenology of the plant rather than the calendar date. Susceptibility to topkilling in particular should be higher during the active growing season than during the dormant season, particularly in deciduous species.

Numerous studies examining the ability of hardwoods to resprout following top-removal or girdling provide evidence for seasonal fluctuations in the ability of plant to recover, independent of any fire-temperature effects. Wenger (1953) and Hare (1961) reviewed the literature on effect of season on coppicing. They conclude that cutting at the time of most active growth in the spring or early summer generally results in the poorest recovery of deciduous hardwoods, and winter cutting results in most vigorous sprouting. All the hardwoods of interest in the Miami Rock Ridge pineland are evergreen or nearly so. It might be expected that evergreen species, since they maintain leaves that can photosynthesize throughout the year, might be more stressed by winter topkilling relative to dormant deciduous species.

Longhurst (1956) observed sprouting ability of two evergreen and two deciduous species of California oaks cut at different times of the year. He suggested that the evergreen species were less sensitive to season of cutting than the deciduous species, although by two years after cutting there appeared to be no seasonal differences among the species in the number of stumps with > 5 sprouts. Juniper (a conifer) cut at various times throughout the year in Texas has less sprout biomass a year after cutting in late May-August than the rest of the year (Schuster and George 1969). In South Florida, coppicing of exotic, evergreen *Eucalyptus* species, in terms of survival of rootstocks and height and biomass of sprouts, was strongly influenced by month of cutting and was lowest in August (Rockwood et al. 1984). With *E. grandis* the biomass of sprouts, although lowest after cutting in August, was depressed for trees cut in the entire July-October period.

Variation in the ability to recover after topkilling is usually attributed to differences in available carbohydrate reserves in the regenerating organ. Deciduous trees generally show a decline and minimum in belowground carbohydrates during the period of leaf enlargement. This is the case with two deciduous oak species in western Florida that showed minima in April and May (Woods et al. 1959). However root carbohydrate levels returned to fairly high levels by June or July, well within the summer fire

period. Evergreen species seem to have lowest reserves later in the year. *Serenoa repens* (admittedly not a hardwood) had lowest available carbohydrate levels in the rhizome in June and July (Hough 1965). *Ilex glabra* in Georgia has lower carbohydrate concentrations in its rhizomes during June, August, and October than January or April (Hughes and Knox 1964).

Evidence that carbohydrate reserves determine the potential capacity of hardwoods to recover from topkilling is not overly convincing. Wenger (1953) speculated that the resprouting of sweetgum may be regulated by the hormonal balance of the plant or by photoperiod because he did not find a good correlation between sprouting vigor and carbohydrate concentration. A study by Jones and Laude (1960) found the least sprouting of *Adenostoma fasciculatum* (chamise) after cutting in May when the carbohydrate content of the roots was relatively high. Although carbohydrate reserves may show a seasonal pattern that is in a general way similar to sprouting ability, it is preferable to conduct cutting experiments to determine directly the variation in recovery ability.

In many pine-hardwood situations, the temperature and physiological factors operate concurrently to result in less recovery after summer fires than winter fires. In subtropical pinelands it is likely that both these factors are not influential because ambient temperatures show

less seasonal fluctuation and the species are evergreen. Individual fire characteristics can therefore more easily override the influence of season.

Fuel moisture conditions in South Florida follow a seasonal pattern that can lead to "cooler" fires during the wet season (summer) than the dry season (winter). The significantly lower hardwood recovery after the early March burn than the September burn in site 2 is due, at least in part, to a large difference in fire temperatures. In this case the lower fuel moisture resulted in higher fire temperatures during the cooler season. A similar phenomenon has been reported in the regeneration of heather in Scotland. Miller and Miles (1970) found that Calluna vulgaris regenerated better after cutting in the spring than the autumn, but better after burning in autumn than spring. This was apparently due to drier conditions in the spring resulting in more severe burns.

It is possible, however, that a physiological mechanism was involved as well in the poor recovery of the hardwoods after the dry season burn at site 2. Even though the available evidence indicates that sprouting ability and carbohydrate reserves of evergreen species reach a minimum in the summer, some of the hardwoods were beginning stem elongation at the time of the March burn and may have been especially susceptible.

### Regrowth Vegetation as a Nutrient Sink

Frequently burned ecosystems, often nutrient-poor ecosystems, must contend with relatively large pulses of nutrients released in leachable or easily mineralizable form in the ash. One mechanism that reduces the losses of this material is the exchange processes and other chemical reactions that hold the nutrients in the soils. Another mechanism whereby nutrients are immobilized within the ecosystem is uptake by the postfire plant community. Nutrients contained in plant biomass are not so subject to leaching or runoff losses as those in the soil. This can be considered a general response of ecosystems to disturbance (Marks and Borman 1972, Vitousek and Reiners 1975) whether the disturbance is fire, logging, insect defoliation, etc. It has even been suggested that the rapid growth of spring ephemerals in temperate deciduous forests is responsible for picking up nutrients that otherwise might be leached and lost from the system (Muller and Borman 1976, Blank et al. 1980). Regrowth vegetation after disturbance may also reduce nutrient losses by other mechanisms. For example, evapotranspiration decreases the amount of water moving through the system and thereby reduces leaching loss (Boerner and Formann 1982). Regrowth of symbiotic N-fixers can also serve to replace some of the N lost through volatilization,

The resprouting mode of recovery may be particularly advantageous in nutrient-poor ecosystems, such as most pinelands, because the established root systems (and possibly stored carbohydrates) allow more rapid initial uptake of nutrients than recovery by seedling regeneration (Chapin and Van Cleve 1981).

In this study the recovery of understory vegetation mass after 1 yr averaged 47% of the original amount. This would represent a substantial amount of nutrients even if nutrient concentrations were the same in regrowth biomass as in the preburn vegetation. However, the higher nutrient concentrations of young tissues (except Ca) mean the immobilization of nutrients was more rapid than biomass accumulation during the first year. At the end of 1 yr of recovery the average standing crops of nutrients in vegetation as a percent of initial standing crop was 52% for N, 60% for P, 55% for K, 46% for Ca, and 56% for Mg. Only Ca, which is unlikely to be limiting in this situation, was not substantially higher than biomass. It is likely that some of the nutrients in the regrowth vegetation are translocated from belowground parts, but by 1 yr they probably represent net uptake by the plants.

The sprouting habit and the pattern of rapid growth by herbs and palms and then hardwoods would seem to make this nutrient-poor system particularly well-adapted to relatively frequent fires. The quick growth by the understory

vegetation should capture the pulse of nutrients released by fire and subsequent decomposition. The turnover of the understory vegetation (through litter production) in the order (from fastest to slowest) herbs, palms, and larger hardwoods should then gradually release nutrients that can be taken up by the pine overstory as well as the understory vegetation. If the fire frequency were to be drastically decreased, the elimination of the herbaceous understory would reduce the ability of the system to retain nutrients after fires. Under a very high fire frequency the herbaceous component of the understory vegetation would increase at the expense of the woody species. The rapid recovery of herbaceous species would presumably be able to retain the nutrients released in smaller but more frequent pulses.

#### Summary and Conclusions

The Miami Rock Ridge pineland is a floristically and ecologically distinctive ecosystem that is perpetuated by frequent fires. The ecosystem itself may be considered endangered because only a few thousand hectares of the original area are maintained in a natural condition, and most of the rest has been irrevocably altered. The plant community contains several endemic taxa, many of which are found in the study plots. Over 128 species were present in the plots, including almost 50 shrubby hardwood species.

Guettarda scabra was the dominant shrub in terms of biomass at both sites. The shrub layer also included three palms and a cycad. The remainder of the species were herbs, with grasses contributing most to biomass.

The burns were backing fires that gave good fuel consumption (> 70%) except for the wet season burn in site 2 where high fuel moisture reduced consumption to about 50%. All the fires completely topkilled the understory vegetation with little immediately visible damage to the overstory. There was little mortality of understory shrubs, but most of the pines < 7 cm dbh in the site 2 dry season burn plot were dead at the end of 1 yr. Fire temperatures were hotter in the site 1 wet season and the site 2 dry season burns than the other burns.

The burns consumed about 1 kg/m<sup>2</sup> of organic matter except in the site 2 dry season burn where about 1.5 kg/m<sup>2</sup> burned. Nitrogen losses ranged from 5.7-9.5 g/m<sup>2</sup>. The N loss can easily be replaced by meteorological inputs and symbiotic and nonsymbiotic fixation during the period of a 3.5-6 yr burning rotation. Losses of cations (K, Ca, Mg) and P were too small to be detected by preburn and postburn sampling, except for one burn where the loss of K was significant. The 78-95 g/m<sup>2</sup> of ash deposited on the soil surface included up to 20 g/m<sup>2</sup> of Ca. The soil pH was still elevated 1 yr after the burns in spite of initial soil pH > 6.0.

The regrowth of the understory vegetation, essentially all by sprouting, was quite rapid. The recovery of nutrient standing crops was faster than biomass because of elevated nutrient concentrations in the regrowth tissues. Herbs and palms began to grow immediately after the burns and reached preburn biomass levels by 1 yr. In some cases the herb and shrub nutrient standing crops were not significantly different from preburn amounts at 2 mo postburn. Hardwoods, whose sprouts appeared later, reached 18-39% of initial biomass and higher levels of nutrients by 1 yr. The recovery of biomass by the total understory vegetation was 27-63%, but the recovery of photosynthetically active tissues (herbs, palms, and hardwood leaves) was an impressive 53-93%.

The rapid vegetative recovery of the understory vegetation probably aids in the retention of the large pulse of nutrients released by the fires.

The litter present 1 yr after burning consisted mostly of vegetation killed in the burns, the heavier pine litter that was not consumed in the burns, and the accumulation of postburn pine litterfall, which was 305-444 g/m<sup>2</sup>. Needlefall (240-326 g/m<sup>2</sup>) made up the bulk of the litterfall. Pine litter constitutes the major portion of the fuel mass.

In the year following burning there was vigorous reproductive activity by the herbs (including several

endemic taxa) but little flowering by the hardwoods. Pine seedling reproduction was greatly favored by wet season burning before the early autumn seedfall.

Even though there were no differences in the degree of topkilling among the four burns or in the recovery of herbs and palms, there were striking differences in the amount of hardwood recovery at the end of 1 yr. However, in one pair of burns the hardwoods in the wet season burn plot recovered less than those in the dry season burn plot and in the other pair the opposite occurred.

I conclude that the season of burning has less impact on hardwood recovery than the specific conditions (especially fuel moisture) under which a burn occurs. The physical and physiological factors that influence response to fire show less seasonal variation in subtropical Florida than at higher latitudes. The dry season burn at site 2 was very hot because a relatively large amount of dry fuel burned. The paired wet season burn had lower fire temperatures because higher fuel moisture limited combustion, even though ambient temperature was higher. Consequently there was significantly less hardwood recovery after the dry season burn.

Natural area management requires making decisions about the desired state of the natural area and how that state is to be maintained. As Bonnicksen and Stone (1982) point out, in natural areas where the ecosystem has been altered by human interference, simply reintroducing natural processes

(such as wet season fires) may not be the way to return to natural conditions. Before natural processes (or prescribed imitations thereof) can operate successfully, the system must be returned to its original state. In the case of the rock ridge pinelands in Everglades National Park the hardwoods may have been less important and the herb layer better developed before interference during the last few decades. To return to these conditions may require more extreme measures than have been attempted by park managers in the past.

Natural fires may have occurred every 3-5 yr in grassy pineland with scattered small hardwoods. But the same fire regime today may do nothing to reduce the amount of hardwoods found after logging and a period of fire suppression. To reduce the hardwoods to their original level may require the use of hot fires followed by very frequent burning. Once a condition considered appropriate is attained the natural fire regime can be reinstated.

There is also, unfortunately, uncertainty about the natural fire regime. The importance of lightning fires is obvious, and it is generally assumed that potential ignitions show the same pattern today as they did in the past. The role of indigenous people in increasing fire frequency and changing the season of burning is, however, less easily evaluated. Upper and lower limits to fire frequency can be inferred from the time it takes for the

endemic herbaceous plants to be shaded out by the shrubby vegetation and the time it takes for sufficient fuel to accumulate, respectively. Reasonable estimates might be 10-15 yr and 2-3 yr. One potential way to address the question of season of burning is to examine the response of individual species to different fire regimes. In particular, plants endemic to rock ridge pinelands should show life history characteristics attuned to the natural occurrence of fires, but this has not been studied. Pine seedling establishment is obviously aided by a wet season burn the year of a good seed crop, although this event need only occur very infrequently.

In lieu of a firm decision on what the natural fire regime was, a conservative approach to prescribed burning seems wise. The rock ridge pinelands recover vigorously after wet or dry season fires and, as long as fires are frequent enough (maybe every 3-7 yr) to prevent further development of hardwoods, the characteristic herbaceous flora should flourish. Wet season lightning fires must have occurred naturally, but it is possible that the endemic flora evolved under conditions that included frequent dry season fires set by indigenous people. By maintaining diversity in the frequency and season of burning there is less likelihood of inadvertently eliminating certain species. It may turn out that fire management plans will be dictated more by the need to discourage the widespread

invasion of the pinelands by the exotic hardwood, Schinus terebinthifolius, than by the desire to encourage native species. With luck, however, these two objectives can be met with the same actions.

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APPENDIX A  
VASCULAR PLANT TAXA PRESENT IN STUDY PLOTS

Table 13. Vascular plant species found in the study plots.  
 Nomenclature follows Avery and Loope (1980b).  
 Woody vines are included with hardwoods.

Taxon	Site 1		Site 2	
	Wet season burn plot	Dry season burn plot	Wet season burn plot	Dry season burn plot
HERBS				
<b>Ferns</b>				
<u>Anemia adiantifolia</u>	*	*	*	*
<u>Pteridium aquilinum</u> var. <u>caudatum</u>	*	*	*	*
<u>Pteris longifolia</u> var. <u>bahamensis</u>	*	*	*	*
<u>Thelypteris kunthii</u>				*
<b>Dicots</b>				
<u>Acalypha chamaedrifolia</u>	*	*	*	*
<u>Agalinis purpurea</u>	*	*	*	*
<u>Angadenia sagraei</u>	*	*	*	*
<u>Asclepias tuberosa</u> ssp. <u>rolfssii</u>				*
<u>Aster adnatus</u>	*	*	*	*
<u>Aster dumosus</u>				*
<u>Ayenia euphrasiifolia</u>	*	*	*	*
<u>Borreria terminalis</u> ( <u>Spermacoce verticillata</u> )	*	*	*	*
<u>Buchnera floridana</u>	*	*	*	*
<u>Carica papaya</u> (exotic, postburn weed)				*
<u>Cassia aspera</u> (exotic)		*		
<u>Cassia deeringiana</u>	*	*	*	*
<u>Cassytha filiformis</u>	*	*	*	*
<u>Centrosema virginianum</u>	*	*		
<u>Chamaesyce adenoptera</u>	*	*		
<u>Chamaesyce pinetorum</u>	*	*	*	*
<u>Chaptalia dentata</u>	*	*		
<u>Chiococca parvifolia</u>	*	*	*	*
<u>Cirsium horridulum</u>	*	*	*	*
<u>Crotalaria pumila</u>	*	*	*	*
<u>Cynanchum blodgettii</u>	*	*	*	
<u>Desmodium lineatum</u>	*	*		
<u>Dyschoriste oblongifolia</u> var. <u>angusta</u>	*	*	*	*
<u>Echites umbellata</u>	*	*	*	*

Table 13. continued

Taxon	Site 1		Site 2	
	Wet season burn plot	Dry season burn plot	Wet season burn plot	Dry season burn plot
				*
<u>Erechtites hieracifolia</u>				
<u>Eupatorium capillifolium</u>			*	
<u>Galactia</u> sp.		*		
<u>Galium hispidulum</u>		*		
<u>Hedyotis nigricans</u> var. <u>filifolia</u>	*	*	*	*
<u>Heterotheca graminifolia</u> var. <u>tracyi</u>	*	*		
<u>Hyptis alata</u> var. <u>stenophylla</u>	*	*	*	*
<u>Ipomea tenuissima</u>	*	*		*
<u>Jacquemontia curtisiae</u>	*	*	*	*
<u>Liatris gracilis</u>	*	*	*	*
<u>Mecardonia acuminata</u>			*	
<u>Melanthera parvifolia</u>	*	*	*	
<u>Mikania scandens</u>		*	*	*
<u>Passiflora suberosa</u>	*	*	*	*
<u>Phyllanthus pentaphyllus</u> var. <u>floridanus</u>	*	*	*	*
<u>Physalis pubescens</u> (postburn weed)			*	
<u>Physalis viscosa</u>	*	*	*	*
<u>Piriqueta caroliniiana</u> var. <u>tomentosa</u>	*	*	*	*
<u>Poinsettia pinetorum</u>	*	*	*	*
<u>Polygala grandiflora</u>	*	*	*	*
<u>Rhynchosia reniformis</u>	*	*		*
<u>Ruellia caroliniensis</u> ssp. <u>ciliosa</u> var. <u>heteromorpha</u>	*	*	*	*
<u>Sachsia polyccephala</u>	*	*	*	*
<u>Samolus ebracteatus</u>		*	*	*
<u>Scutellaria havanensis</u>				*
<u>Solidago chapmanii</u>	*	*		
<u>Solidago stricta</u>	*		*	*
<u>Stillingia sylvatica</u> ssp. <u>tenuis</u>	*	*		
<u>Tephrosia florida</u>	*	*		
<u>Tragia saxicola</u>	*	*	*	*
<u>Vernonia blodgettii</u>	*	*	*	

Table 13. continued

Taxon	Site 1		Site 2	
	Wet season burn plot	Dry season burn plot	Wet season burn plot	Dry season burn plot
<b>Monocots</b>				
<u>Andropogon cabanisii</u>	*	*	*	*
<u>Aristida spp.</u>	*	*	*	*
<u>Cladium jamaicensis</u>			*	*
<u>Dicanthelium sp.</u>	*	*		
<u>Dichromena floridensis</u>	*	*	*	*
<u>Digitaria spp.</u>	*	*		
<u>Muhlenbergia capillaris</u>	*	*	*	*
<u>Panicum spp.</u>		*	*	
<u>Paspalum setaceum</u>	*	*	*	*
<u>Rhynchospora globularis</u>		*		
<u>Schizachyrium gracile</u>	*	*	*	
<u>Schizachyrium rhizomatum</u>	*	*	*	*
<u>Schizachyrium semiberbe</u>	*	*		
<u>Scleria ciliata</u>	*	*		
<u>Sorghastrum secundum</u>	*	*	*	*
<u>Tripsicum floridanum</u>			*	
<b>SHRUBS</b>				
<b>Cycads</b>				
<u>Zamia pumila</u>	*	*		*
<b>Palms</b>				
<u>Coccothrinax argentata</u>	*	*		*
<u>Sabal palmetto</u>	*	*	*	*
<u>Serenoa repens</u>	*	*	*	*
<b>Hardwoods</b>				
<u>Ardisia escallonioides</u>	*	*	*	*
<u>Baccharis glomeruliflora</u>		*	*	
<u>Bumelia reclinata</u> var. <u>reclinata</u>		*	*	*
<u>Bumelia salicifolia</u>	*	*	*	*
<u>Byrsonima lucida</u>	*	*	*	*
<u>Callicarpa americana</u>	*	*		*
<u>Chrysobalanus icaco</u>			*	*
<u>Chrysophyllum oliviforme</u>			*	*

Table 13. continued

Taxon	Site 1		Site 2	
	Wet season burn plot	Dry season burn plot	Wet season burn plot	Dry season burn plot
<u>Citharexylum fruticosum</u>	*	*		
<u>Coccocloba diversifolia</u>			*	*
<u>Colubrina arborescens</u>		*	*	*
<u>Crossopetalum ilicifolium</u>	*		*	*
<u>Croton linearis</u>	*	*	*	
<u>Dodonaea viscosa</u> var. <u>linearis</u>	*	*	*	*
<u>Eugenia axillaris</u>		*	*	*
<u>Eupatorium villosum</u>			*	*
<u>Exothea paniculata</u>			*	
<u>Ficus citrifolia</u>	*	*	*	*
<u>Forestiera segregata</u> var. <u>pinetorum</u>			*	*
<u>Guapira discolor</u>	*	*	*	*
<u>Guettarda elliptica</u>	*	*	*	*
<u>Guettarda scabra</u>	*	*	*	*
<u>Ilex cassine</u>			*	*
<u>Ilex krugiana</u>	*	*	*	*
<u>Jacquinia keyensis</u>			*	
<u>Lantana depressa</u>	*	*	*	*
<u>Lantana involucrata</u>	*	*	*	
<u>Licania michauxii</u>	*	*		*
<u>Lysiloma latifolia</u>			*	*
<u>Metopium toxiferum</u>	*	*	*	*
<u>Morinda royoc</u>	*	*	*	*
<u>Myrcianthes fragrans</u> var. <u>simpsonii</u>				*
<u>Myrica cerifera</u>	*	*	*	*
<u>Myrsine floridana</u>	*	*	*	*
<u>Persea borbonia</u>	*		*	*
<u>Psidium longipes</u>	*	*	*	*
<u>Psychotria nervosa</u>			*	
<u>Quercus virginiana</u>			*	*
<u>Randia aculeata</u>	*	*	*	*
<u>Rhus copallina</u>	*	*	*	*
<u>Schinus terebinthifolius</u> (exotic)		*		*
<u>Simarouba glauca</u>		*		
<u>Smilax auriculata</u>	*	*	*	*
<u>Smilax bona-nox</u>				*
<u>Tetrazygia bicolor</u>	*	*	*	*

Table 13. continued

Taxon	Site 1		Site 2	
	Wet season burn plot	Dry season burn plot	Wet season burn plot	Dry season burn plot
<u>Toxicodendron radicans</u>		*	*	
<u>Trema micrantha</u>	*	*	*	*
<u>Vitis aestivalis</u>			*	
<u>Vitis munsoniana</u>		*	*	*

APPENDIX B  
STANDING CROPS OF DRY MASS AND NUTRIENTS

The following tables show the standing crops of dry mass and nutrients (N, P, K, Ca, and Mg) before burning, immediately after burning, and at 2, 7, and 12 mo after burning. The immediate postburn vegetation is that part of the initial vegetation not consumed by the fire, but is actually dead and is part of the understory litter. Values are means with standard errors in parentheses. Sample sizes are  $n = 24$  and  $n = 12$  for dry mass at site 1 and site 2, respectively. For all nutrient standing crops  $n = 4$ . Differences between sampling periods were tested by one-way ANOVA and Waller-Duncan multiple comparisons ( $K = 100$ , SAS Institute Inc. 1992) on log 10 transformed data. Sampling periods with the same superscript are not significantly different.

Table 14. Dry mass standing crops, site 1 wet season burn plot.

VEGETATION	COMPARTMENT	DRY MASS ( $\text{g/m}^2$ )			
		PREBURN	POSTBURN	2 MONTH	7 MONTH
SHRUBS					
Cycads ( <i>Zamia pumila</i> )	193.8 (15.5) <sup>a</sup>	98.5 (13.2)	13.7 (13.1) <sup>d</sup>	46.9 (6.70) <sup>c</sup>	81.7 (8.95) <sup>b</sup>
Palms	4.0 (1.18)	--	0.2 (0.06)	0.6 (0.23)	1.3 (0.56)
Sabal Palmetto	42.1 (18.06) <sup>a</sup>	--	10.4 (3.23) <sup>b</sup>	36.1 (6.86) <sup>a</sup>	51.4 (9.29) <sup>a</sup>
Serenoa repens	16.4 (5.41)	--	2.1 (1.50)	10.0 (3.40)	12.1 (3.97)
Coccothrinax argenteata	21.9 (6.62)	--	8.7 (2.90)	25.8 (6.41)	36.0 (8.74)
3.8 (2.67)	--	0.1 (0.12)	0.2 (0.23)	3.3 (1.94)	
HARDWOODS					
Leaves	147.7 (16.84) <sup>a</sup>	--	2.6 (0.50) <sup>d</sup>	10.2 (1.81) <sup>c</sup>	29.0 (2.85) <sup>b</sup>
Stems	55.5 (7.17)	--	--	--	17.5 (1.57)
92.2 (10.03)	70.7 (10.08)	--	--	--	11.5 (1.14)
Guettarda scabra	68.9 (10.94)	--	0.5 (0.10)	4.9 (1.09)	12.7 (1.50)
Leaves	24.0 (3.74)	--	--	--	8.4 (0.94)
Stems	44.9 (7.26)	--	--	--	4.3 (0.58)
Dodonaea viscosa	30.8 (4.28)	--	0.9 (0.19)	1.9 (0.42)	
Leaves	10.3 (1.42)	--	--	--	2.5 (0.51)
Stems	20.5 (2.90)	--	--	--	1.6 (0.40)
HERBS					
41.2 (3.83) <sup>a</sup>	8.7 (2.88)	16.5 (1.95) <sup>c</sup>	36.0 (5.79) <sup>b</sup>	48.1 (3.38) <sup>a</sup>	
VEGETATION TOTAL	235.0 (14.98) <sup>a</sup>	107.2 (14.00)	30.2 (3.13) <sup>d</sup>	82.9 (8.41) <sup>c</sup>	129.8 (10.26) <sup>b</sup>
LITTER					
FINE					
888.7 (56.04) <sup>a</sup>	177.2 (27.01)	175.6 (15.9) <sup>d</sup>	303.4 (30.67) <sup>c</sup>	471.0 (25.21) <sup>b</sup>	
Needles	673.2 (33.77)	--	75.2 (4.18)	140.5 (6.99)	278.6 (9.98)
Other	215.5 (34.65)	--	100.4 (13.90)	163.0 (28.52)	192.4 (19.56)
UNDERSTORY					
292.8 (22.73) <sup>a</sup>	0.1 (0.13)	91.8 (14.87) <sup>c</sup>	100.2 (14.01) <sup>bc</sup>	112.8 (9.99) <sup>b</sup>	
Shrub	--	--	91.8 (14.87)	100.2 (14.01)	86.3 (10.02)
Forest floor	--	--	--	48.2 (9.05)	37.8 (5.34)
Standing dead	--	--	<0.1	52.2 (9.05)	48.5 (6.8)
Herb	--	--	<0.1	<0.1	26.5 (2.77)
LITTER TOTAL	1181.5 (53.96) <sup>a</sup>	177.3 (26.98)	267.4 (21.17) <sup>d</sup>	403.6 (32.72) <sup>c</sup>	583.8 (29.71) <sup>b</sup>
GRAND TOTAL	1416.5 (54.78) <sup>a</sup>	284.5 (22.43) <sup>d</sup>	297.6 (22.43) <sup>d</sup>	486.5 (33.56) <sup>c</sup>	713.6 (29.97) <sup>b</sup>

Table 15. Dry mass standing crops, site 1 dry season burn plot.

VEGETATION	COMPARTMENT		DRY MASS (g/m <sup>2</sup> )		
	PREBURN	POSTBURN	2 MONTH	7 MONTH	12 MONTH
SHRUBS					
Cycads ( <i>Zamia fumata</i> )	170.3(14.63) <sup>a</sup>	163.3(21.94)	8.7(1.29) <sup>c</sup>	90.2(10.56) <sup>b</sup>	93.9(10.39) <sup>b</sup>
Palms	3.1(1.26)	--	0.1(0.05)	0.2(0.12)	0.6(0.29)
<i>Sabal</i> <u>palmetto</u>	39.5(10.44) <sup>a</sup>	--	6.2(1.22) <sup>b</sup>	35.9(7.27) <sup>a</sup>	43.5(9.35) <sup>a</sup>
<i>Serenoa repens</i>	16.8(8.00)	--	1.3(0.90)	9.9(4.71)	5.4(2.11)
<i>Coccothrinax argenteata</i>	21.6(7.01)	--	4.9(1.00)	23.9(7.21)	38.0(9.86)
1.1(0.59)	--	<0.1	0.1(0.07)	0.1(0.10)	
HARDWOODS					
Leaves	127.6(12.05) <sup>a</sup>	--	2.4(0.41) <sup>c</sup>	54.1(5.68) <sup>b</sup>	49.8(5.32) <sup>b</sup>
Stems	40.9(4.11)	--	--	--	29.1(2.70)
86.7(8.20)	119.9(17.16)	--	--	--	20.6(3.18)
<u>Guettarda scabra</u>	63.9(9.67)	--	<0.1	27.1(3.54)	27.2(4.33)
Leaves	24.0(3.12)	--	--	--	17.2(2.75)
Stems	39.9(6.55)	--	--	--	10.0(1.64)
<u>Dodonaea viscosa</u>	35.3(4.62)	--	1.1(0.22)	7.0(1.10)	7.3(1.24)
Leaves	9.3(1.31)	--	--	--	4.3(0.74)
Stems	26.1(3.47)	--	--	--	3.0(0.52)
HERBS					
30.0(3.19) <sup>a</sup>	0.9(0.36)	7.8(1.04) <sup>b</sup>	36.6(3.45) <sup>a</sup>	32.6(2.62) <sup>a</sup>	
200.3(3.19) <sup>a</sup>	164.2(21.95)	16.5(1.25) <sup>c</sup>	126.8(10.21) <sup>b</sup>	126.5(10.85) <sup>b</sup>	
VEGETATION TOTAL,					
LITTER					
PINE					
904.3(49.50) <sup>a</sup>	140.3(20.16)	161.3(12.48) <sup>d</sup>	339.6(16.05) <sup>c</sup>	468.4(29.51) <sup>b</sup>	
Needles					
Other	773.3(40.71)	--	71.9(7.89)	203.1(9.23)	270.9(9.31)
131.0(22.98)	--	89.4(10.89)	136.4(15.74)	197.6(27.38)	
UNDERSTORY					
228.1(27.01) <sup>a</sup>	2.5(1.04)	130.3(15.95) <sup>b</sup>	120.4(14.20) <sup>b</sup>	143.7(9.10) <sup>b</sup>	
Shrub					
Forest floor	--	138.3(15.95)	112.3(14.68)	104.3(10.89)	
Standing dead	--	--	43.8(12.11)	28.9(6.45)	36.5(5.99)
Herb	--	--	94.5(18.59)	83.4(12.40)	67.5(7.89)
LITTER TOTAL,	1132.4(46.92) <sup>a</sup>	142.8(20.18)	290.7(20.33) <sup>d</sup>	460.0(18.34) <sup>c</sup>	612.2(29.17) <sup>b</sup>
GRAND TOTAL,	1332.7(49.74) <sup>a</sup>	307.0(28.76)	316.2(20.99) <sup>d</sup>	586.8(24.14) <sup>c</sup>	738.7(30.42) <sup>b</sup>

Table 16. Dry mass standing crops, site 2 wet season burn plot.

VEGETATION	DRY MASS (g/m <sup>2</sup> )			
	PREBURN	POSTBURN	2 MONTH	7 MONTH
SUBURBS				
Palms	434.1(31.77) <sup>a</sup>	385.3(102.57)	17.8(1.54) <sup>d</sup>	61.7(6.72) <sup>c</sup>
Sabal Palmetto	38.6(6.81) <sup>a</sup>	27.6(3.43)	13.3(1.44) <sup>b</sup>	24.0(2.70) <sup>ab</sup>
<u>Serenia Repens</u>	30.7(7.15) <sup>a</sup>	--	7.6(1.25)	19.4(3.10)
8.0(4.08)	--	--	5.8(1.80)	4.6(2.16)
Hardwoods	395.5(31.19) <sup>a</sup>	357.7(101.75)	4.5(0.87) <sup>d</sup>	37.7(5.44) <sup>c</sup>
Leaves	120.1(8.47) <sup>a</sup>	86.1(22.38)	--	137.4(20.96) <sup>b</sup>
Stems	275.4(26.50)	271.6(80.33)	--	81.4(11.94)
Guettarda scabra	108.8(15.14) <sup>a</sup>	93.1(13.56)	0.3(0.08)	56.0(9.89)
leaves	31.4(5.26) <sup>a</sup>	22.3(4.06)	--	31.3(8.41)
stems	77.4(10.30)	70.9(10.49)	--	20.7(5.45)
HERBS	21.8(5.59) <sup>a</sup>	0.9(0.63)	4.6(0.72) <sup>c</sup>	11.4(1.67) <sup>b</sup>
VEGETATION TOTAL	456.0(31.33) <sup>a</sup>	386.2(103.05)	22.4(1.38) <sup>d</sup>	73.1(5.99) <sup>c</sup>
LITTER				
PINE	994.8(93.40) <sup>a</sup>	393.8(66.55)	311.2(39.90) <sup>c</sup>	324.5(27.04) <sup>bc</sup>
Needles	795.0(65.24)	--	--	403.2(28.14) <sup>b</sup>
Other	199.8(64.20)	--	--	156.1(10.88)
UNIVERSTORY	457.9(70.45) <sup>a</sup>	66.5(50.54)	351.9(129.28) <sup>a</sup>	168.4(22.27)
Shrub	--	--	351.9(129.28)	353.7(51.77) <sup>a</sup>
Forest floor	--	--	72.9(17.18)	353.7(51.77) <sup>a</sup>
Standing dead	--	--	279.0(116.39)	487.2(97.45)
Herb	--	--	<0.1	157.7(49.29)
LITTER TOTAL	1452.7(93.59) <sup>a</sup>	460.3(83.47)	663.1(121.38) <sup>c</sup>	241.5(41.26)
GRAND TOTAL	1908.7(112.66) <sup>a</sup>	846.5(165.29)	685.5(121.62) <sup>c</sup>	678.1(55.58) <sup>bc</sup>
				329.5(66.81)
				11.7(2.51)
				992.1(103.03) <sup>b</sup>
				1090.8(118.45) <sup>b</sup>

Table 17. Dry mass standing crops, site 2 dry season burn plot.

VEGETATION	COMPARTMENT	DRY MASS (g/m <sup>2</sup> )			
		PREBURN	POSTBURN	2 MONTH	8 MONTH
SHRUBS					
Palms	472.0(82.95) <sup>a</sup>	375.5(43.01)	10.8(1.40) <sup>c</sup>	111.8(9.46) <sup>b</sup>	120.2(11.19) <sup>b</sup>
Sabal palmetto	43.4(10.35) <sup>a</sup>	6.4(2.20)	8.5(1.63) <sup>b</sup>	31.2(6.86) <sup>a</sup>	41.9(7.88) <sup>a</sup>
Serenoa repens	26.2(6.21)	--	7.1(1.35)	19.3(4.02)	25.9(3.16)
17.2(8.73)	--	--	1.4(0.68)	11.9(5.32)	16.0(6.33)
Hardwoods	428.6(83.76) <sup>a</sup>	369.1(42.80)	2.3(0.42) <sup>c</sup>	80.6(8.80) <sup>b</sup>	78.3(8.49) <sup>b</sup>
Leaves	10.4(18.19)	50.9(7.35)	--	--	40.9(4.29)
Stems	328.2(65.63)	310.2(40.38)	--	--	37.4(4.42)
Guettarda scabra	125.7(29.93)	74.9(11.00)	0.04(0.003)	18.3(3.76)	31.2(7.20)
Leaves	32.2(7.76)	10.0(2.07)	--	--	15.8(3.68)
Stems	93.4(22.97)	64.9(9.31)	--	--	15.5(3.54)
HERBS	18.9(4.05) <sup>a</sup>	<0.1	1.5(0.26) <sup>b</sup>	15.4(2.91) <sup>a</sup>	11.2(1.91) <sup>a</sup>
VEGETATION TOTAL	490.9(81.43) <sup>a</sup>	375.5(43.01)	12.3(1.45) <sup>c</sup>	127.3(8.41) <sup>b</sup>	131.4(10.47) <sup>b</sup>
LITTER					
PINE	1220.6(96.21) <sup>a</sup>	49.0(11.26)	124.9(12.97) <sup>c</sup>	344.0(27.00) <sup>b</sup>	396.2(35.82) <sup>b</sup>
Needles	1037.2(81.73)	--	85.7(4.26)	241.3(11.62)	287.1(12.15)
Other	18.4(22.10)	--	39.3(10.57)	102.6(19.68)	109.1(33.94)
UNDERSTORY					
Shrub	264.1(60.68) <sup>a</sup>	9.4(4.27)	375.1(84.38) <sup>a</sup>	328.6(43.24) <sup>a</sup>	223.5(44.34) <sup>a</sup>
Forest floor	--	--	375.1(84.38)	324.5(42.76)	211.0(45.14)
Standing dead	--	--	94.6(17.97)	73.1(14.83)	78.1(9.77)
Herb	--	--	<0.1	25.4(32.99)	132.9(39.66)
LITTER TOTAL	1484.7(80.37) <sup>a</sup>	58.4(13.99)	500.0(80.54) <sup>c</sup>	672.6(54.10) <sup>b</sup>	619.7(59.50) <sup>b</sup>
GRAND TOTAL	1975.7(1107.51) <sup>a</sup>	433.9(47.85)	512.3(79.76) <sup>c</sup>	799.9(57.41) <sup>b</sup>	751.1(63.64) <sup>b</sup>

Table 18. Nitrogen standing crops, site 1 wet season burn plot.

VEGETATION	COMPARTMENT	NITROGEN (mg/m <sup>2</sup> )			
		PREBURN	POSTBURN	2 MONTH	7 MONTH
<u>SHRUBS</u>					
Palms	1492(135.9) <sup>a</sup>	473(1121.5)	216(26.6) <sup>d</sup>	606(87.3) <sup>c</sup>	851(40.7) <sup>b</sup>
<u>Sabal palmetto</u>	446(121.7) <sup>a</sup>	--	163(24.6) <sup>b</sup>	458(103.6) <sup>a</sup>	544(57.1) <sup>a</sup>
<u>Sereno repens</u>	193(101.3)	--	37(22.6)	153(72.7)	155(95.6)
<u>Coccothrinax argenteata</u>	212(81.5)	--	153(20.2)	302(31.9)	349(63.2)
41(23.7)	--	2(11.9)	4(3.1)	39(29.4)	
Hardwoods	1046(221.0) <sup>a</sup>	--	53(13.9) <sup>d</sup>	148(23.7) <sup>c</sup>	307(19.9) <sup>b</sup>
Leaves	730(157.5)	--	--	--	--
Stems	316(65.1)	219(45.0)	--	--	--
<u>Glettarda scabra</u>	399(86.4)	--	9(3.1)	61(14.5)	118(6.1)
Leaves	269(58.7)	--	--	--	98(4.9)
Stems	130(28.2)	--	--	--	19(1.4)
<u>Bodonaea viscosa</u>	254(2.2)	--	17(2.4)	--	44(11.6)
Leaves	166(3.9)	--	--	--	37(9.1)
Stems	87(4.2)	--	--	--	8(2.5)
HERBS	324(21.0) <sup>ab</sup>	53(7.6)	244(32.5) <sup>b</sup>	357(48.6) <sup>ab</sup>	414(25.7) <sup>a</sup>
VEGETATION TOTAL.	1815(141.9) <sup>a</sup>	526(112.9)	466(22.4) <sup>d</sup>	963(103.1) <sup>c</sup>	1265(37.3) <sup>b</sup>
LITTER					
PINE	4592(624.5) <sup>a</sup>	547(140.1)	481(12.6) <sup>d</sup>	907(71.8) <sup>c</sup>	1449(53.6) <sup>b</sup>
Needles	3744(601.8)	--	214(10.2)	452(24.3)	950(18.9)
Other	848(115.6)	--	266(9.7)	455(65.1)	499(47.7)
UNDERSTORY	2897(443.7) <sup>a</sup>	2(1.5)	507(92.9) <sup>b</sup>	612(57.5) <sup>b</sup>	622(29.5) <sup>b</sup>
Shrub	--	--	507(92.9)	612(53.5)	496(31.6)
Forest floor	--	--	--	307(31.5)	
Standing dead	--	--	--	<1	312(26.0)
Herb	--	--	--	<1	185(26.6)
LITTER TOTAL.	7489(980.5) <sup>a</sup>	549(1139.2)	988(99.4) <sup>d</sup>	1519(117.8) <sup>c</sup>	2071(29.1) <sup>b</sup>
GRAND TOTAL	9304(1094.2) <sup>a</sup>	1075(65.5)	1449(118.3) <sup>d</sup>	2482(205.0) <sup>c</sup>	3336(50.7) <sup>b</sup>

Table 19. Nitrogen standing crops, site 1 dry season burn plot.

VEGETATION	NITROGEN (mg/m <sup>2</sup> )					
	COMPARTMENT	PREBURN	POSTBURN	2 MONTH	7 MONTH	12 MONTH
SHRUB						
<i>Palms</i>						
<i>Sabal Palmetto</i>	1386 (180.2) <sup>a</sup>	832 (125.1)	160 (127.5) <sup>b</sup>	1030 (183.0) <sup>a</sup>	941 (70.5) <sup>a</sup>	941 (70.5) <sup>a</sup>
<i>Serenoa repens</i>	458 (125.7) <sup>a</sup>	--	102 (19.3) <sup>b</sup>	441 (110.2) <sup>a</sup>	491 (93.6) <sup>a</sup>	491 (93.6) <sup>a</sup>
<i>Coccothrinax argenteata</i>	230 (93.0)	--	19 (1.1) <sup>b</sup>	--	--	--
<i>10 (7.1)</i>	218 (39.1)	--	83 (9.5)	--	--	--
<i>10 (7.1)</i>	10 (7.1)	--	<1	--	--	--
<i>Hardwoods</i>						
<i>Leaves</i>	928 (131.8) <sup>a</sup>	--	58 (9.2) <sup>d</sup>	589 (84.5) <sup>c</sup>	450 (41.3) <sup>b</sup>	348 (38.9)
<i>Stems</i>	546 (83.0)	--	--	--	--	103 (10.4)
<i>382 (53.0)</i>	382 (53.0)	496 (67.7)	--	--	--	103 (10.4)
<i>Guettarda scabra</i>						
<i>Leaves</i>	434 (85.6)	--	--	275 (20.6)	230 (61.1)	230 (61.1)
<i>Stems</i>	260 (52.6)	--	--	--	185 (49.1)	185 (49.1)
<i>Dodonaea viscosa</i>						
<i>Leaves</i>	174 (33.2)	--	--	--	45 (12.0)	45 (12.0)
<i>Stems</i>	273 (46.3)	--	25 (2.7)	84 (8.0)	76 (12.5)	76 (12.5)
<i>151 (29.6)</i>	151 (29.6)	--	--	--	62 (10.0)	62 (10.0)
<i>121 (17.0)</i>	121 (17.0)	--	--	--	14 (2.5)	14 (2.5)
HERBS						
<i>258 (47.3) b</i>	6 (2.6)	126 (12.5) <sup>b</sup>	317 (10.2) <sup>ab</sup>	260 (22.1) <sup>a</sup>	260 (22.1) <sup>a</sup>	260 (22.1) <sup>a</sup>
VEGETATION TOTAL	1643 (180.4) <sup>a</sup>	838 (123.3)	286 (15.9) <sup>d</sup>	1347 (175.8) <sup>c</sup>	1202 (56.0) <sup>b</sup>	1202 (56.0) <sup>b</sup>
LITTER						
PINE						
<i>Needles</i>	4420 (366.6) <sup>a</sup>	513 (65.4)	722 (114.4) <sup>d</sup>	1131 (62.2) <sup>c</sup>	1523 (155.2) <sup>b</sup>	1523 (155.2) <sup>b</sup>
<i>Other</i>	3712 (562.9)	--	397 (117.3)	758 (72.1)	999 (70.5)	999 (70.5)
<i>707 (204.3)</i>	707 (204.3)	--	325 (9.3)	373 (61.1)	524 (85.9)	524 (85.9)
UNDERSTORY						
Shrub						
<i>Forest floor</i>	1636 (157.9) <sup>a</sup>	17 (5.5)	619 (99.1) <sup>b</sup>	642 (80.6) <sup>b</sup>	740 (54.0) <sup>b</sup>	740 (54.0) <sup>b</sup>
<i>Standing dead</i>	--	--	619 (99.1)	597 (88.8)	579 (44.1)	579 (44.1)
<i>Herb</i>	--	--	215 (53.0)	232 (41.6)	303 (23.7)	303 (23.7)
LITTER TOTAL	6056 (382.5) <sup>a</sup>	530 (70.1)	1341 (122.8) <sup>d</sup>	1773 (47.0) <sup>c</sup>	2263 (184.4) <sup>b</sup>	2263 (184.4) <sup>b</sup>
GRAND TOTAL	7699 (431.2) <sup>a</sup>	1367 (156.3)	1626 (1134.8) <sup>d</sup>	3120 (199.6) <sup>c</sup>	3464 (218.5) <sup>b</sup>	3464 (218.5) <sup>b</sup>

Table 20. Nitrogen standing crops, site 2 wet season burn plot.

VEGETATION	COMPARTMENT	NITROGEN (mg/m <sup>2</sup> )			
		PREBURN	POSTBURN	2 MONTH	7 MONTH
SHRUB					
Palms	2840(77.6) <sup>a</sup>	2263(623.6)	302(38.7) <sup>d</sup>	894(66.6) <sup>c</sup>	1744(189.2) <sup>b</sup>
Sabal palmetto	402(102.0) <sup>a</sup>	266(58.3)	212(34.8) <sup>b</sup>	359(46.2) <sup>a</sup>	370(62.5) <sup>a</sup>
Serenoa repens	335(111.7)	--	126(11.7)	30(49.2)	--
Leaves	68(22.8)	--	67(12.9)	58(36.4)	--
Stems	1418(65.8) <sup>a</sup>	1997(651.6)	90(23.6) <sup>d</sup>	535(42.6) <sup>c</sup>	1374(162.9) <sup>b</sup>
Leaves	1415(75.7)	897(30.7)	--	--	105(14.2) <sup>a</sup>
Stems	1023(27.9)	1099(351.4)	--	--	320(39.3)
Guettarda scabra					
Leaves	553(41.7)	451(31.8)	5(1.2)	66(16.3)	300(61.4)
Stems	333(25.6)	220(29.5)	--	--	252(51.0)
Leaves	219(17.5)	231(14.4)	--	--	48(10.5)
HERBS					
175(57.1) <sup>ab</sup>	6(5.7)	78(12.9) <sup>b</sup>	146(9.4) <sup>ab</sup>	219(24.9) <sup>a</sup>	
VEGETATION TOTAL		3015(100.7) <sup>a</sup>	2269(628.8)	380(35.1) <sup>d</sup>	1040(71.5) <sup>c</sup>
LITTER					
PINE					
Needles	7550(1321.1) <sup>a</sup>	1533(249.1)	1222(139.6) <sup>b</sup>	1208(172.4) <sup>b</sup>	1356(164.8) <sup>b</sup>
Other	6634(1092.4)	--	--	622(92.3)	919(63.8)
UNDERSTORY					
Shrub	916(1379.5)	--	--	586(190.8)	437(115.5)
Forest floor	3573(429.0) <sup>a</sup>	545(413.5)	1812(527.8) <sup>b</sup>	2110(127.2) <sup>b</sup>	2410(1315.6) <sup>ab</sup>
Standing dead	--	--	1812(527.8)	2110(127.2)	2342(312.6)
Herb	--	--	613(122.5)	1068(141.2)	1034(285.9)
LITTER TOTAL		11,123(905.0) <sup>a</sup>	2078(612.8)	<1	1309(256.3)
GRAND TOTAL		14,138(941.0) <sup>a</sup>	4347(1237.8)	3414(592.7) <sup>c</sup>	68(10.8)
GRAND TOTAL				3318(219.3) <sup>b</sup>	3767(168.1) <sup>b</sup>
				4358(202.0) <sup>b</sup>	5729(327.4) <sup>b</sup>

Table 21. Nitrogen standing crops, site 2 dry season burn plot.

VEGETATION	COMPARTMENT		NITROGEN (mg/m <sup>2</sup> )		
	PREBURN	POSTBURN	2 MONTH	8 MONTH	12 MONTH
<b>SHRUB</b>					
Palms	3186(983.1) <sup>a</sup>	2290(512.3)	172(14.1) <sup>c</sup>	1416(88.3) <sup>b</sup>	1279(193.3) <sup>b</sup>
Sabal <u>palmietto</u>	461(147.4) <sup>a</sup>	37(13.6)	129(14.4) <sup>b</sup>	482(126.3) <sup>a</sup>	522(153.1) <sup>a</sup>
<u>Sextonia repens</u>	319(85.7)	--	108(9.3)	--	--
Hardwoods	2725(955.8) <sup>a</sup>	2252(512.3)	43(7.4) <sup>c</sup>	933(136.7) <sup>b</sup>	757(89.3) <sup>b</sup>
Leaves	1193(402.7)	665(137.9)	--	--	538(64.9)
Stems	1532(555.5)	1538(389.4)	--	--	219(25.0)
Guettarda <u>scabra</u>	65(147.6)	332(41.7)	--	196(27.6)	270(56.0)
Leaves	308(81.0)	99(21.1)	--	--	192(41.6)
Stems	337(71.2)	233(23.6)	--	--	78(14.5)
Herbs	184(45.0) <sup>a</sup>	<1	27(3.8) <sup>b</sup>	170(22.6) <sup>a</sup>	133(15.2) <sup>a</sup>
VEGETATION TOTAL	3370(949.3) <sup>a</sup>	2290(512.3)	199(17.7) <sup>c</sup>	1586(93.8) <sup>b</sup>	1413(196.6) <sup>b</sup>
<b>LITTER</b>					
PINE	7200(1019.7) <sup>a</sup>	189(61.5)	421(41.8) <sup>c</sup>	1052(64.5) <sup>b</sup>	1227(108.8) <sup>b</sup>
Needles	6290(1097.1)	--	390(13.1)	759(53.3)	928(74.7)
Other	910(188.4)	--	131(28.8)	293(30.4)	300(103.4)
UNDERSTORY	2774(688.6) <sup>a</sup>	118(72.4)	2111(525.5) <sup>a</sup>	1712(234.4) <sup>a</sup>	1393(235.6) <sup>a</sup>
Shrub	--	--	2111(525.5)	1693(226.6)	1345(243.1)
Forest floor	--	--	682(175.5)	630(98.9)	701(137.4)
Standing dead	--	--	1429(366.4)	1062(134.7)	643(153.9)
Herb	--	--	<1	191(10.1)	48(21.3)
LITTER TOTAL	9975(1489.1) <sup>a</sup>	307(133.3)	2532(496.5) <sup>b</sup>	2764(215.6) <sup>b</sup>	2620(309.0) <sup>b</sup>
GRAND TOTAL	13,345(1805.1) <sup>a</sup>	2597(575.5)	2730(483.7) <sup>c</sup>	4350(1265.7) <sup>b</sup>	4033(424.0) <sup>b</sup>

Table 22. Phosphorus standing crops, site 1 wet season burn plot.

COMPARTMENT	PHOSPHORUS (mg/m <sup>2</sup> )		
	PREBURN	POSTBURN	7 MONTH
<b>VEGETATION</b>			
SHRUBS	95.7(10.29) <sup>a</sup>	36.3(7.81)	17.2(1.98) <sup>c</sup>
Palms	26.0(7.43) <sup>ab</sup>	--	13.3(1.58) <sup>b</sup>
<i>Sabal Palmetto</i>	12.0(6.37)	--	3.5(2.17)
<i>Serenia Repens</i>	11.5(4.35)	--	9.7(1.24)
<i>Coccothrinax Argentata</i>	2.5(1.43)	--	0.1(0.14)
Hardwoods	69.7(15.19) <sup>a</sup>	--	3.9(0.96) <sup>d</sup>
Leaves	40.2(8.20)	--	8.8(1.39) <sup>c</sup>
Stems	29.5(7.16)	19.2(3.72)	18.9(0.81) <sup>b</sup>
<i>Guettarda Scabra</i>	29.1(7.43)	--	--
Leaves	15.2(3.37)	--	0.7(0.21)
Stems	13.9(4.08)	--	--
<i>Dodonaea Viscosa</i>	16.8(0.31)	--	1.4(0.19)
Leaves	9.4(0.19)	--	1.5(0.26)
Stems	7.4(0.35)	--	--
HERBS	21.6(1.65) <sup>a</sup>	4.0(0.68)	17.4(2.75) <sup>a</sup>
Vegetation Total	117.4(11.10) <sup>a</sup>	40.4(7.70)	34.6(2.31) <sup>c</sup>
LITTER			
PINE	109.8(12.54) <sup>a</sup>	21.6(5.93)	16.2(0.85) <sup>d</sup>
Needles	91.7(12.80)	--	8.1(0.62)
Other	18.1(1.09)	--	8.1(0.42)
UNDERSTORY	56.2(5.41) <sup>a</sup>	<0.1	27.3(5.57) <sup>b</sup>
Shrub	--	--	--
Forest floor	--	--	26.4(3.38) <sup>b</sup>
Standing dead	--	--	18.6(1.96)
Herb	--	--	16.2(2.33)
LITTER TOTAL	166.0(13.67) <sup>a</sup>	21.6(5.91)	43.5(5.96) <sup>c</sup>
GRAND TOTAL	283.4(20.95) <sup>a</sup>	62.0(2.61)	78.1(7.88) <sup>c</sup>
			120.1(11.77) <sup>b</sup>
			148.2(4.51) <sup>b</sup>

Table 23. Phosphorus standing crops, site 1 dry season burn plot.

VEGETATION	PHOSPHORUS (mg/m <sup>2</sup> )			
	PREBURN	POSTBURN	2 MONTH	7 MONTH
<b>CARPARTMENT</b>				
SHRUBS				
Palms	84.2(11.15) <sup>a</sup>	54.3(11.23)	13.2(2.33) <sup>b</sup>	61.5(10.57) <sup>a</sup>
Sabal Palmetto	27.7(7.09) <sup>a</sup>	--	8.9(1.65) <sup>b</sup>	54.6(3.96) <sup>a</sup>
Serenoa repens	14.9(5.51)	--	1.9(1.11)	27.9(5.63) <sup>a</sup>
Coccothrinax argenteata	12.2(1.88)	--	7.0(0.78)	--
0.7(0.47)	--	<0.1	--	--
Hardwoods	56.4(7.59) <sup>a</sup>	--	4.3(0.77) <sup>c</sup>	26.6(3.07) <sup>b</sup>
Leaves	27.2(4.23)	--	33.6(3.82) <sup>b</sup>	17.3(1.99)
Stems	29.2(3.92)	32.9(6.84)	--	9.4(1.48)
Gutterkoda scabra	24.3(4.83)	--	--	16.8(1.48)
leaves	11.7(2.33)	--	--	13.9(4.08)
stems	12.6(2.55)	--	--	9.0(2.40)
Dodonaea viscosa	18.8(3.40)	--	2.0(0.17)	4.9(1.72)
leaves	9.1(1.88)	--	--	4.3(0.66)
stems	9.7(1.56)	--	--	3.2(0.59)
HERBS	15.8(2.48) <sup>a</sup>	0.4(0.19)	10.1(0.98) <sup>b</sup>	20.4(0.68) <sup>a</sup>
VEGETATION TOTAL	100.0(10.90) <sup>a</sup>	54.7(11.13)	23.3(1.71) <sup>c</sup>	81.9(9.71) <sup>ab</sup>
LITTER				
PINE	104.3(9.58) <sup>a</sup>	17.9(1.91)	33.9(6.78) <sup>c</sup>	41.4(2.46) <sup>bc</sup>
Needles	92.3(7.86)	--	22.5(7.28)	54.9(6.07) <sup>b</sup>
Other	12.0(2.63)	--	11.4(0.55)	37.4(3.35)
UNDERSTORY	47.9(11.94) <sup>a</sup>	0.5(0.26)	46.2(10.48) <sup>a</sup>	12.1(1.05)
Shrub	--	--	32.2(4.02) <sup>a</sup>	17.6(2.94)
Forest floor				
Standing dead				
Herb	--	--	46.2(10.48)	29.4(3.31) <sup>a</sup>
LITTER TOTAL	152.1(15.27) <sup>a</sup>	16.5(2.13)	80.1(11.85) <sup>b</sup>	73.6(12.51) <sup>b</sup>
GRAND TOTAL	252.1(15.00) <sup>a</sup>	73.1(12.43)	103.4(13.50) <sup>c</sup>	155.5(11.71) <sup>b</sup>
				154.7(10.47) <sup>b</sup>

Table 24. Phosphorus standing crops, site 2 wet season burn plot.

COMPARTMENT	PREBURN	POSTBURN	PHOSPHORUS (mg/m <sup>2</sup> )		
			2 MONTH	7 MONTH	12 MONTH
<b>VEGETATION</b>					
SHRUBS	153.9(4.05) <sup>a</sup>	126.0(33.05)	21.8(2.52) <sup>d</sup>	53.7(4.63) <sup>c</sup>	84.5(7.11) <sup>b</sup>
Palms	25.6(7.92) <sup>a</sup>	17.1(3.23)	14.8(2.05) <sup>a</sup>	21.5(2.65) <sup>a</sup>	21.1(3.56) <sup>a</sup>
<u>Sabal palmetto</u>	22.0(6.42)	--	9.2(0.91)	18.1(2.32)	3.3(12.02)
<u>Serenoa repens</u>	3.1(1.27)	--	5.5(2.03)	--	--
Hardwoods	128.3(4.29) <sup>a</sup>	108.9(35.16)	7.0(1.82) <sup>d</sup>	32.2(3.82) <sup>c</sup>	63.4(5.04) <sup>b</sup>
Leaves	66.1(3.28)	43.3(14.29)	--	--	42.1(4.34)
Stems	62.2(1.44)	65.6(21.13)	--	--	21.3(1.60)
<u>Guettarda scabra</u>	32.2(2.06)	27.3(2.34)	0.4(0.09)	4.0(1.01)	15.1(3.07)
leaves	17.7(1.26)	13.0(1.99)	--	--	11.1(2.14)
stems	14.5(1.07)	14.3(10.64)	--	--	3.9(0.98)
HERBS	10.5(3.59) <sup>a</sup>	0.2(0.22)	5.3(0.81) <sup>a</sup>	7.7(0.70) <sup>a</sup>	10.8(1.55) <sup>a</sup>
VEGETATION TOTAL	164.4(5.63) <sup>a</sup>	126.3(33.26)	27.1(1.95) <sup>d</sup>	61.4(5.16) <sup>c</sup>	95.3(7.65) <sup>b</sup>
<b>LITTER</b>					
PINE	130.1(9.11) <sup>a</sup>	51.0(9.03)	40.5(5.14) <sup>b</sup>	41.3(5.89) <sup>b</sup>	40.0(5.21) <sup>b</sup>
Needles	115.0(5.97)	--	--	23.9(3.97)	27.8(2.38)
Other	15.1(4.40)	--	--	17.4(2.64)	12.3(3.04)
UNDERSTORY	83.3(7.83) <sup>a</sup>	13.0(9.94)	82.4(16.43) <sup>a</sup>	85.5(3.76) <sup>a</sup>	73.0(8.35) <sup>a</sup>
Shrub	--	--	82.4(16.42)	65.5(3.76)	70.5(8.26)
Forest floor	--	--	32.4(23.58)	38.8(3.00)	31.9(6.33)
Standing dead	--	--	58.2(15.24)	46.6(2.16)	38.7(4.23)
Herb	--	--	<0.1	<0.1	2.5(0.38)
LITTER TOTAL	213.4(5.22) <sup>a</sup>	64.0(17.28)	122.9(18.47) <sup>b</sup>	126.8(7.01) <sup>b</sup>	113.1(4.25) <sup>b</sup>
GRAND TOTAL	377.9(10.79) <sup>a</sup>	190.3(50.11)	150.0(19.00) <sup>c</sup>	188.2(7.27) <sup>b</sup>	208.4(10.00) <sup>b</sup>

Table 25. Phosphorus standing crops, site 2 dry season burn plot.

VEGETATION	PHOSPHORUS (mg/m <sup>2</sup> )					
	COMPARTMENT	PREBURN	POSTBURN	2 MONTH	8 MONTH	12 MONTH
SHRUBS						
Palms	157.4(24.68) <sup>a</sup>	113.3(16.14)	12.7(1.07) <sup>c</sup>	77.4(4.04) <sup>b</sup>	75.3(10.11) <sup>b</sup>	
Sabal Palmetto	27.6(8.60) <sup>a</sup>	3.2(1.16) <sup>j</sup>	9.5(1.14) <sup>b</sup>	28.7(7.08) <sup>a</sup>	30.4(8.65) <sup>a</sup>	
<i>Serenita repens</i>	19.5(5.18) <sup>a</sup>	--	8.1(1.08)	1.4(0.89)	--	--
Hardwoods	8.1(3.51)	--	--	--	--	--
Leaves	129.8(23.33) <sup>a</sup>	110.1(16.26)	3.2(0.63) <sup>c</sup>	48.7(5.17) <sup>b</sup>	44.9(4.43) <sup>b</sup>	
Stems	48.9(10.76)	29.9(5.19)	--	--	28.8(3.12)	
80.9(13.17)	80.2(11.62)	--	--	--	18.0(1.73)	
Quettarda scabra	37.9(7.75)	20.7(2.65)	--	10.4(1.57)	15.5(2.75)	
leaves	14.4(3.57)	4.7(1.02)	--	--	9.1(1.89)	
stems	23.4(4.25)	16.0(2.05)	--	--	6.4(0.86)	
HERBS	9.8(2.58) <sup>a</sup>	<0.1	1.7(0.30) <sup>b</sup>	8.4(1.40) <sup>a</sup>	5.9(0.74) <sup>a</sup>	
VEGETATION TOTAL	167.2(22.87) <sup>a</sup>	113.3(16.14)	14.4(1.33) <sup>c</sup>	85.8(3.19) <sup>b</sup>	81.1(9.88) <sup>b</sup>	
LITTER						
FINE	158.2(6.06) <sup>a</sup>	5.8(1.85)	16.0(1.68) <sup>c</sup>	34.4(2.78) <sup>b</sup>	41.9(5.92) <sup>b</sup>	
Needles	139.1(4.53)	--	11.9(0.67)	25.8(2.34)	31.0(3.45)	
Other	19.1(1.91)	--	4.1(1.01)	8.6(0.90)	10.8(4.84)	
UNDERSTORY	53.6(12.80) <sup>b</sup>	1.9(1.14)	10.2(9.23.34) <sup>d</sup>	56.3(7.11)ab	50.4(6.73) <sup>b</sup>	
Shrub	--	--	102.9(23.34)	55.4(6.87)	48.8(7.12)	
Forest floor	--	--	33.8(5.07)	20.5(2.80)	24.6(4.70)	
Standing dead	--	--	69.2(16.98)	35.0(4.11)	24.2(4.21)	
Herb	--	--	<0.1	1.0(0.51)	1.6(0.73)	
LITTER TOTAL	211.8(12.73) <sup>a</sup>	7.7(2.98)	118.9(22.12) <sup>b</sup>	90.8(6.57) <sup>b</sup>	92.3(11.33) <sup>b</sup>	
GRAND TOTAL	379.0(34.48) <sup>a</sup>	121.0(18.00)	133.3(21.33) <sup>c</sup>	176.6(8.91) <sup>b</sup>	173.4(17.32) <sup>bc</sup>	

Table 26. Potassium standing crops, site 1 wet season burn plot.

VEGETATION	POTASSIUM (mg/m <sup>2</sup> )			
	PREBURN	POSTBURN	2 MONTH	7 MONTH
<b>COMPARTMENT</b>				
SHRUBS	1258(129.4) <sup>a</sup>	532(131.4)	185(23.4) <sup>c</sup>	494(82.3) <sup>b</sup>
Palms	309(97.9) <sup>ab</sup>	--	140(21.9) <sup>b</sup>	588(33.2) <sup>b</sup>
<i>Sabal palmetto</i>	15(85.2)	--	29(117.1)	322(39.0) <sup>a</sup>
<i>Serenoa repens</i>	12(31.0)	--	108(25.0)	97(57.6)
<i>Coccothrinax argenteata</i>	30(17.5)	--	21(8.8)	196(32.1)
HARDWOODS	949(189.5) <sup>a</sup>	--	45(121.1) <sup>d</sup>	114(16.4) <sup>c</sup>
Leaves	638(107.8)	--	--	266(17.0) <sup>b</sup>
Stems	32(181.9)	241(51.6)	--	--
<i>Gnetum scabrum</i>	431(101.9)	--	8(2.7)	52(8.6)
Leaves	309(67.4)	--	--	125(7.6)
Stems	122(35.5)	--	--	95(7.7)
<i>Bodonaea viscosa</i>	197(2.7)	--	--	30(2.5)
Leaves	134(3.7)	--	15(1.9)	20(3.7)
Stems	63(1.3)	--	--	38(11.1)
HERBS	373(20.4) <sup>a</sup>	80(13.8)	266(52.4) <sup>b</sup>	287(50.7) <sup>a</sup>
VEGETATION TOTAL	1631(132.8) <sup>a</sup>	612(129.7)	451(46.8) <sup>c</sup>	781(114.3) <sup>b</sup>
LITTER				
PINE	180(23.6) <sup>a</sup>	48(8.5)	51(8.7) <sup>c</sup>	87(9.8) <sup>b</sup>
Needles	154(22.6)	--	34(7.2)	43(3.5)
Other	26(4.3)	--	17(1.5)	45(7.7)
UNDERSTORY	146(16.4) <sup>a</sup>	<1	121(29.0) <sup>a</sup>	69(13.2) <sup>a</sup>
Shrub	--	--	--	82(17.3) <sup>a</sup>
Forest floor	--	--	--	69(13.2) <sup>a</sup>
Standing dead	--	--	--	34(6.3)
Herb	--	--	--	35(8.8)
LITTER TOTAL	325(9.0) <sup>a</sup>	48(8.5)	172(35.9) <sup>b</sup>	157(19.5) <sup>b</sup>
GRAND TOTAL	1956(133.7) <sup>a</sup>	660(122.1)	623(60.5) <sup>c</sup>	938(119.1) <sup>b</sup>
				1187(44.5) <sup>b</sup>

Table 27. Potassium standing crops, site 1 dry season burn plot.

COMPARTMENT <sup>a</sup>	POTASSIUM (mg/m <sup>2</sup> )			
	PREBURN	POSTBURN	2 MONTH	7 MONTH
<b>VEGETATION</b>				
SHRUBS	955(161.5) <sup>a</sup>	704(118.2)	130(27.7) <sup>b</sup>	819(157.8) <sup>a</sup>
Palms	285(69.9) <sup>a</sup>	--	87(21.0) <sup>b</sup>	643(57.0) <sup>a</sup>
<i>Sabal palmetto</i>	161(55.0)	--	20(5.1) <sup>b</sup>	273(62.1) <sup>a</sup>
<i>Serenia repens</i>	117(18.1)	--	66(9.3)	--
<i>Coccolithoxia argentata</i>	7(5.4)	--	<1	--
Hardwoods	670(138.5) <sup>a</sup>	--	43(7.3) <sup>c</sup>	497(73.2) <sup>ab</sup>
Leaves	389(81.9)	--	--	370(35.8) <sup>b</sup>
Stems	282(47.1)	361(53.2)	--	254(35.2)
<i>Guettarda scabra</i>	214(77.7)	--	--	116(13.3)
Leaves	214(53.9)	--	--	--
Stems	12(24.1)	--	--	--
<i>Dodonaea viscosa</i>	17(139.3)	--	--	--
Leaves	10(23.1)	--	21(2.0)	68(8.1)
Stems	6(16.4)	--	--	--
HERBS	312(40.1) <sup>a</sup>	6(3.0)	134(17.8) <sup>b</sup>	290(8.2) <sup>a</sup>
VEGETATION TOTAL	1266(161.7) <sup>a</sup>	709(116.7)	264(18.7) <sup>b</sup>	1109(153.7) <sup>a</sup>
<b>LITTER</b>				
PINE	216(38.9) <sup>a</sup>	48(12.2)	93(10.6) <sup>c</sup>	64(4.2) <sup>d</sup>
Needles	172(34.0)	--	62(15.2)	40(2.0)
Other	44(11.6)	--	31(8.6)	24(4.3)
UNDERSTORY	219(41.2) <sup>ab</sup>	2(0.9)	438(136.3) <sup>a</sup>	86(13.2) <sup>c</sup>
Shrub	--	--	438(136.3)	76(15.7)
Forest floor	--	--	194(10.2)	16(4.2)
Standing dead	--	--	244(40.0)	60(13.9)
Herb	--	--	<1	11(3.4)
LITTER TOTAL	435(133.7) <sup>a</sup>	51(12.3)	531(135.5) <sup>a</sup>	150(11.3) <sup>c</sup>
GRAND TOTAL	1702(163.9) <sup>a</sup>	760(128.5)	794(144.7) <sup>b</sup>	1259(162.8) <sup>a</sup>
				1140(70.1) <sup>a</sup>

Table 28. Potassium standing crops, site 2 wet season burn plot.

VEGETATION	COMPARTMENT	POTASSIUM (mg/m <sup>2</sup> )			
		PREBURN	POSTBURN	2 MONTH	7 MONTH
SHRUBS					
Palms	1274 (97.8) <sup>a</sup>	1185 (304.5)	193 (16.5) <sup>d</sup>	574 (44.1) <sup>c</sup>	795 (60.9) <sup>b</sup>
Sabal Palmetto	258 (108.7) ab	196 (24.4)	123 (6.9) <sup>b</sup>	246 (11.1) <sup>a</sup>	162 (32.7) ab
<i>Serenoa repens</i>	237 (109.9)	--	77 (10.5)	219 (6.0)	--
Hardwoods	21 (4.7)	--	46 (16.9)	26 (18.3)	--
Leaves	1016 (12.3) <sup>a</sup>	990 (327.5)	69 (17.6) <sup>c</sup>	328 (35.1) <sup>b</sup>	637 (39.5) <sup>a</sup>
Stems	598 (16.3)	393 (113.2)	--	--	413 (33.3)
<i>Guettarda scabra</i>	418 (6.9)	597 (21.8)	--	--	224 (15.3)
leaves	319 (31.1)	292 (29.5)	6 (1.6)	58 (12.1)	192 (40.1)
stems	234 (17.5)	165 (19.5)	--	--	148 (30.1)
HERBS	86 (14.9)	126 (15.0)	--	--	44 (9.9)
LITTER	122 (38.6) ab	2 (2.2)	67 (10.3) <sup>b</sup>	92 (7.2) <sup>ab</sup>	133 (13.4) <sup>a</sup>
VEGETATION TOTAL,	1396 (109.8) <sup>a</sup>	1167 (306.6)	260 (8.5) <sup>d</sup>	665 (45.4) <sup>c</sup>	932 (63.5) <sup>b</sup>
PINE					
Needles	132 (17.5) <sup>a</sup>	59 (10.6)	48 (8.8) <sup>b</sup>	65 (9.5) <sup>b</sup>	52 (4.4) <sup>b</sup>
Other	120 (16.3)	--	--	37 (5.4)	39 (2.8)
12 (3.5)	--	--	28 (5.5)	13 (2.7)	
UNDERSTORY					
Shrub	136 (16.1) b	21 (16.4)	313 (86.4) <sup>a</sup>	232 (10.1) <sup>ab</sup>	199 (26.4) <sup>ab</sup>
Forest floor	--	--	313 (86.4)	232 (10.1)	185 (23.4)
Standing dead	--	--	44 (11.5)	59 (7.1)	39 (9.9)
Herb	--	--	269 (89.1)	173 (10.3)	146 (16.7)
LITTER TOTAL,	268 (15.0) <sup>a</sup>	80 (24.1)	<1	<1	14 (3.7)
GRAND TOTAL,	1664 (113.2) <sup>a</sup>	1268 (327.1)	361 (91.9) <sup>a</sup>	297 (10.7) <sup>a</sup>	251 (27.3) <sup>a</sup>
			621 (89.8) <sup>c</sup>	963 (46.4) <sup>b</sup>	1183 (79.2) <sup>b</sup>

Table 29. Potassium standing crops, site 2 dry season burn plot.

COMPARTMENT	POTASSIUM (mg/m <sup>2</sup> )		
	PREBURN	POSTBURN	2 MONTH
<b>VEGETATION</b>			
SHRUBS	1120(128.7) <sup>a</sup>	709(69.4)	124(8.5) <sup>c</sup>
Palms	205(47.4) <sup>ab</sup>	47(16.3)	95(10.6) <sup>b</sup>
<i>Sabal palmetto</i>	157(13.8)	--	61(14.5)
<i>Serenoa repens</i>	48(11.5)	--	14(7.4)
Hardwoods	915(118.7) <sup>a</sup>	662(72.3)	29(5.1) <sup>c</sup>
Leaves	382(64.8)	157(19.1)	--
Stems	533(58.0)	505(58.7)	--
Guettarda <i>scabra</i>	343(32.1)	132(20.7)	--
Leaves	156(25.7)	27(6.9)	--
Stems	185(18.9)	110(15.5)	--
HERBS	97(27.5) <sup>a</sup>	<1	21(3.5) <sup>b</sup>
VEGETATION TOTAL	1217(111.5) <sup>a</sup>	709(69.4)	145(10.3) <sup>c</sup>
LITTER			
PINE	171(6.8) <sup>a</sup>	8(2.8)	26(3.7) <sup>d</sup>
Needles	149(10.1)	--	20(2.1)
Other	22(3.8)	--	5(1.7)
UNIVERSTORY			
Shrub	79(20.4) <sup>c</sup>	3(1.5)	625(211.3) <sup>a</sup>
Forest floor	--	--	625(211.3)
Standing dead	--	--	147(38.4)
Herb	--	--	479(173.5)
LITTER TOTAL	256(26.6) <sup>b</sup>	10(4.3)	651(208.7) <sup>a</sup>
GRAND TOTAL	1467(138.0) <sup>a</sup>	719(72.3)	796(214.3) <sup>b</sup>
			12 MONTH
			8 MONTH
			12 MONTH
			706(50.5) <sup>b</sup>
			221(44.8) <sup>a</sup>
			--
			244(58.7) <sup>a</sup>
			--
			462(39.3) <sup>b</sup>
			271(30.0)
			191(12.3)
			117(15.2)
			--
			189(32.5)
			115(24.3)
			73(8.6)
			64(7.7) <sup>a</sup>
			786(20.5) <sup>b</sup>
			770(47.7) <sup>b</sup>
			84(16.9) <sup>b</sup>
			43(8.4) <sup>c</sup>
			33(8.0)
			10(2.0)
			118(12.2) <sup>bc</sup>
			154(24.1) <sup>b</sup>
			109(10.1)
			23(2.6)
			86(10.5)
			9(5.9)
			161(5.1) <sup>b</sup>
			238(17.7) <sup>b</sup>
			946(14.5) <sup>ab</sup>
			1009(49.7) <sup>ab</sup>

Table 30. Calcium standing crops, site 1 wet season burn plot.

VEGETATION COMPARTMENT	CALCIUM (mg/m <sup>2</sup> )			
	PREBURN	POSTBURN	2 MONTH	7 MONTH
SHRUBS				
Palms	2250(453.4) <sup>a</sup>	1001(289.6)	75(16.7) <sup>d</sup>	358(39.5) <sup>c</sup>
Sabal <u>Palmetto</u>	227(16.9) <sup>a</sup>	--	36(19.4) <sup>b</sup>	771(42.9) <sup>b</sup>
Serenoa <u>repens</u>	110(152.6)	--	13(7.7)	289(55.7) <sup>a</sup>
Coccothrinax <u>argentata</u>	104(47.4)	--	23(4.6)	111(64.8)
13(8.1)	--	--	1(0.7)	163(30.3)
Hardwoods				
Leaves	2023(514.1) <sup>a</sup>	--	39(11.7) <sup>d</sup>	185(30.9) <sup>c</sup>
958(127.5)	--	--	--	482(45.0) <sup>b</sup>
Stems	1065(246.8)	725(198.5)	--	--
Grevillea <u>scabra</u>				
Leaves	673(153.4)	--	6(2.2)	86(17.9)
Stems	229(48.8)	--	--	169(8.5)
Dodonaea <u>viscosa</u>	444(105.7)	--	--	102(4.0)
Leaves	326(8.5)	--	13(1.7)	67(16.1)
Stems	128(4.2)	--	--	49(12.5)
198(7.0)	--	--	--	33(8.6)
HERBS				
292(117.6) <sup>b</sup>	34(9.7)	113(11.4) <sup>c</sup>	291(51.7) <sup>b</sup>	480(40.8) <sup>a</sup>
VEGETATION TOTAL	2542(444.6) <sup>a</sup>	1035(292.2)	188(18.5) <sup>d</sup>	649(76.6) <sup>c</sup>
LITTER				
PINE				
Needles	6049(358.3) <sup>a</sup>	1717(344.1)	1093(49.6) <sup>d</sup>	1933(200.4) <sup>c</sup>
Other	4976(396.1)	--	426(9.7)	906(40.4)
1073(56.8)	--	--	673(52.1)	1027(176.1)
UNDERSTORY				
Shrub				
Forest Floor	3287(449.1) <sup>a</sup>	2(1.6)	1233(285.4) <sup>b</sup>	1119(212.9) <sup>b</sup>
Standing dead	--	--	1233(285.4)	1119(212.9)
Herb	--	--	--	441(62.0)
LITTER TOTAL	9336(1686.9) <sup>a</sup>	1719(1343.8)	2332(329.6) <sup>c</sup>	3052(382.5) <sup>c</sup>
GRAND TOTAL	11,878(929.7) <sup>a</sup>	2734(281.1)	2521(340.1) <sup>d</sup>	4080(138.5) <sup>b</sup>
				3701(448.5) <sup>c</sup>
				5330(120.2) <sup>b</sup>

Table 31. Calcium standing crops, site 1 dry season burn plot.

VEGETATION	COMPARTMENT	CALCIUM ( $\text{mg/m}^2$ )			
		PREBURN	POSTBURN	2 MONTH	7 MONTH
<b>SHRUBS</b>					
<i>Sabal palmetto</i>	2014(273.8) <sup>a</sup>	1686(291.8)	52(9.7) <sup>c</sup>	1052(195.0) <sup>b</sup>	1077(55.8) <sup>b</sup>
<i>Sabal palmetto</i>	268(61.8) <sup>a</sup>	--	21(5.1) <sup>b</sup>	174(49.8) <sup>a</sup>	257(44.5) <sup>a</sup>
<i>Serenoa repens</i>	131(44.6)	--	7(1.5)	--	--
<i>Coccoloba uvifera</i>	126(24.3)	--	14(1.1)	--	--
<i>Coccoloba uvifera</i>	8(5.7)	--	<1	--	--
<b>Hardwoods</b>					
Leaves	1746(227.3) <sup>a</sup>	--	30(4.9) <sup>c</sup>	878(158.8) <sup>b</sup>	820(56.6) <sup>b</sup>
Leaves	758(106.5)	--	--	--	556(15.4)
Stems	989(134.9)	1247(212.0)	--	--	254(24.3)
<i>Guettarda scabra</i>	865(165.9)	--	--	374(41.6)	378(91.6)
leaves	366(61.5)	--	--	--	267(65.7)
stems	499(105.4)	--	--	--	111(26.6)
<i>Dodonaea viscosa</i>	36(155.4)	--	15(2.2)	104(10.7)	85(13.5)
leaves	131(25.4)	--	--	--	58(9.5)
stems	229(52.1)	--	--	--	27(4.2)
<b>HERBS</b>					
Leaves	235(42.8) <sup>a</sup>	3(1.5)	86(22.3) <sup>b</sup>	354(41.0) <sup>a</sup>	294(27.7) <sup>a</sup>
Vegetation Total	2249(263.2) <sup>a</sup>	1689(290.7)	138(26.0) <sup>c</sup>	1406(227.3) <sup>b</sup>	1371(51.0) <sup>b</sup>
<b>LITTER</b>					
PINE	5465(276.4) <sup>a</sup>	1246(136.7)	1142(158.9) <sup>d</sup>	2083(97.9) <sup>c</sup>	2864(226.0) <sup>b</sup>
Needleless	4879(211.6)	--	336(73.3)	1402(60.3)	1746(65.0)
Other	586(137.8)	--	806(91.3)	680(102.0)	1118(192.3)
<b>UNDERSTORY</b>					
Shrub	2332(611.2) <sup>a</sup>	26(9.9)	1526(236.0) <sup>a</sup>	1496(202.0) <sup>a</sup>	1388(180.7) <sup>a</sup>
Forest floor	--	--	1526(236.0)	1429(214.9)	1169(170.7)
Standing dead	--	--	266(74.9)	381(70.1)	509(75.8)
Herb	--	--	1260(1165.4)	1048(170.1)	660(154.8)
Litter Total	7796(442.1) <sup>a</sup>	1272(146.3)	2668(262.5) <sup>c</sup>	3578(167.2) <sup>b</sup>	4252(290.4) <sup>b</sup>
Grand Total	10,046(265.9) <sup>a</sup>	2361(313.4)	2806(275.6) <sup>c</sup>	4984(347.4) <sup>b</sup>	5623(338.0) <sup>b</sup>

Table 32. Calcium standing crops, site 2 wet season burn plot.

VEGETATION	CALCIUM (mg/m <sup>2</sup> )		
	PREBURN	POSTBURN	2 MONTH
SHRUBS			
Palms	5732 (201.0) <sup>a</sup>	5375 (11692.6)	120 (18.8) <sup>d</sup>
Sabal palmata	281 (72.9) <sup>a</sup>	183 (24.2)	63 (5.8) <sup>b</sup>
Serenoa repens	44 (14.9)	--	157 (26.9) <sup>a</sup>
Hardwoods			
Leaves	5446 (262.8) <sup>a</sup>	5192 (1698.6)	18 (3.8) <sup>b</sup>
Stems	2290 (102.7)	1686 (672.9)	18 (6.7) <sup>b</sup>
Guettarda scabra	3116 (183.6)	3506 (11037.2)	27 (14.9) <sup>c</sup>
Leaves	1032 (140.3)	1035 (79.9)	57 (18.6) <sup>d</sup>
Stems	361 (53.1)	275 (37.9)	--
Herbs	711 (98.1)	760 (75.0)	--
VEGETATION TOTAL	221 (55.7) <sup>a</sup>	9 (8.8)	66 (9.8) <sup>b</sup>
LITTER			
PINE	5933 (162.8) <sup>a</sup>	5384 (1700.6)	228 (28.4) <sup>a</sup>
Needles	10,841 (639.5) <sup>a</sup>	185 (11.1) <sup>d</sup>	1149 (116.4) <sup>c</sup>
Other	9200 (377.9)	4638 (928.8)	3655 (1535.3) <sup>b</sup>
UNDERSTORY			
Shrub	8337 (2112.1) <sup>a</sup>	1027 (727.7)	4776 (1404.9) <sup>a</sup>
Forest floor	--	--	4776 (1104.9) <sup>a</sup>
Standing dead	--	--	1373 (219.8) <sup>b</sup>
Herb	--	--	<1 (1161.2)
LITTER TOTAL	19,178 (1595.6) <sup>a</sup>	5665 (1510.6)	8431 (1691.2) <sup>b</sup>
GRAND TOTAL	25,131 (1746.5) <sup>a</sup>	11,049 (3167.1)	8617 (1699.8) <sup>c</sup>
			8917 (238.7) <sup>c</sup>
			13,134 (614.6) <sup>b</sup>
			2826 (223.0) <sup>b</sup>

Table 33. Calcium standing crops, site 2 dry season burn plot.

COMPARTMENT	CALCIUM (mg/m <sup>2</sup> )			
	PREBURN	POSTBURN	2 MONTH	8 MONTH
<b>VEGETATION</b>				
SHRUBS	6769(1622.4) <sup>a</sup>	5514(1105.2)	65(3.5) <sup>c</sup>	1704(1132.7)
Palms	312(108.0) <sup>a</sup>	38(16.1)	46(4.7) <sup>b</sup>	1598(181.7) <sup>b</sup>
<i>Sabal palmetto</i>	210(159.3)	--	41(4.8)	293(73.8) <sup>a</sup>
<i>Serenia repens</i>	102(49.3)	--	5(3.5)	--
Hardwoods	645(1611.7) <sup>a</sup>	5476(1101.8)	19(1.4) <sup>c</sup>	1305(1130.7) <sup>b</sup>
Leaves	219(630.9)	1247(354.0)	--	864(67.9)
Stems	426(998.9)	4230(843.9)	--	441(45.9)
<i>Guettarda scabra</i>	1498(305.4)	837(118.4)	--	369(93.1)
leaves	538(148.5)	169(35.3)	--	205(46.9)
stems	950(165.4)	669(94.6)	--	164(36.4)
HERBS	237(70.7) <sup>a</sup>	<1	46(7.3) <sup>b</sup>	213(67.8) <sup>a</sup>
VEGETATION TOTAL	7006(1570.5) <sup>a</sup>	5514(1105.2)	111(5.0) <sup>c</sup>	156(17.5) <sup>a</sup>
LITTER				
PINE	11,706(1616.8) <sup>a</sup>	510(1113.3)	932(110.0) <sup>c</sup>	2731(56.6) <sup>b</sup>
Needles	10,500(1640.2)	--	538(20.8)	1930(82.1)
Other	1207(59.6)	--	334(9.1)	781(84.5)
UNDERSTORY				
Shrub	435(11235.3) <sup>a</sup>	157(93.1)	5841(1276.9) <sup>a</sup>	3847(481.4) <sup>a</sup>
Forest floor	--	--	5841(1276.9)	3823(470.2)
Standing dead	--	--	1493(316.6)	1285(240.4)
Herb	--	--	4348(11035.9)	2537(231.6)
LITTER TOTAL	16,058(1641.7) <sup>a</sup>	666(201.9)	6774(11160.3) <sup>b</sup>	6578(491.4) <sup>b</sup>
GRAND TOTAL	23,064(12736.8) <sup>a</sup>	6180(11249.1)	6885(11176.2) <sup>b</sup>	8494(1580.5) <sup>b</sup>
				8306(756.3) <sup>b</sup>

Table 34. Magnesium standing crops, site 1 wet season burn plot.

VEGETATION	MAGNESIUM (mg/m <sup>2</sup> )			
	PREBURN	POSTBURN	2 MONTH	7 MONTH
<b>COMPARTMENT<sup>a</sup></b>				
SHRUBS	311(50.1) <sup>a</sup>	119(26.2)	27(4.4) <sup>d</sup>	82(12.4) <sup>c</sup>
Palms	72(23.3) <sup>a</sup>	--	20(3.3) <sup>b</sup>	151(13.5) <sup>b</sup>
<u>Sabal palmetto</u>	36(20.8)	--	63(14.7) <sup>a</sup>	90(15.4) <sup>a</sup>
<u>Serenoa repens</u>	31(14.7)	--	25(1.1)	27(1.6) <sup>b</sup>
<u>Coccothrinax argentata</u>	5(2.9)	--	15(2.9)	38(4.9) <sup>b</sup>
Hardwoods	239(65.9) <sup>a</sup>	--	7(2.0) <sup>d</sup>	<1
Leaves	149(43.8)	--	19(3.6) <sup>c</sup>	61(5.9) <sup>b</sup>
Stems	91(22.5)	66(12.5)	--	--
<u>Guettarda scabra</u>	80(19.4)	--	6(1.3)	--
Leaves	4(10.4)	--	--	17(1.3)
Stems	39(9.2)	--	--	12(0.5)
<u>Dodonaea viscosa</u>	58(2.3)	--	2(0.5)	6(0.5)
Leaves	34(1.2)	--	--	10(2.5)
Stems	24(1.6)	--	--	8(2.0)
HERBS	72(4.6) <sup>a</sup>	11(3.1)	33(5.4) <sup>b</sup>	89(17.1) <sup>a</sup>
VEGETATION TOTAL	383(50.1) <sup>a</sup>	130(26.3)	60(3.7) <sup>d</sup>	171(21.4) <sup>c</sup>
LITTER				257(14.0) <sup>b</sup>
PINE	979(46.7) <sup>a</sup>	125(31.8)	162(5.5) <sup>d</sup>	280(22.1) <sup>c</sup>
Needles	874(44.1)	--	105(3.8)	482(40.8) <sup>b</sup>
Other	105(4.3)	--	57(4.3)	182(8.0)
UNDERSTORY	266(34.4) <sup>a</sup>	<1	107(26.0) <sup>b</sup>	98(11.1)
Shrub	--	--	107(26.0)	96(12.2)
Forest Floor	--	--	--	52(10.1)
Standing dead	--	--	--	33(6.6)
Herb	--	--	<1	43(8.0)
LITTER TOTAL	1245(61.9) <sup>a</sup>	125(31.7)	269(29.2) <sup>d</sup>	376(32.5) <sup>c</sup>
GRAND TOTAL	1629(106.3) <sup>a</sup>	256(16.6)	329(32.1) <sup>d</sup>	546(51.7) <sup>c</sup>
	--	--	--	843(40.9) <sup>b</sup>

Table 35. Magnesium standing crops, site 1 dry season burn plot.

VEGETATION	MAGNESIUM (mg/m <sup>2</sup> )			
	PREBURN	POSTBURN	2 MONTHS	7 MONTHS
<b>COMPARTMENT</b>				
SHRUBS				
Palms	270 (38.5) <sup>a</sup>	208 (32.5)	18 (2.8) <sup>c</sup>	167 (34.3) <sup>b</sup>
<u>Sabal</u> <u>pubescens</u>	76 (20.2) <sup>a</sup>	--	11 (2.0) <sup>b</sup>	166 (16.6) <sup>b</sup>
<u>S. tucumana</u>	42 (13.6) <sup>a</sup>	--	3 (1.8) <sup>b</sup>	75 (16.1) <sup>a</sup>
<u>S. sp.</u>	32 (7.6) <sup>a</sup>	--	8 (0.8) <sup>b</sup>	--
<u>Coccothrinax argenteata</u>	2 (1.0)	--	<1	--
Hardwoods				
Leaves	194 (32.3) <sup>a</sup>	--	7 (1.0) <sup>c</sup>	103 (15.6) <sup>b</sup>
Stems	95 (16.7) <sup>a</sup>	122 (21.4) <sup>a</sup>	--	91 (8.4) <sup>b</sup>
<u>Guettarda scabra</u>	95 (16.8) <sup>a</sup>	--	--	60 (5.2) <sup>b</sup>
Leaves	89 (19.5) <sup>a</sup>	--	--	31 (4.5) <sup>b</sup>
Stems	41 (9.0) <sup>a</sup>	--	--	34 (4.4) <sup>b</sup>
<u>Dodonaea viscosa</u>	48 (10.5) <sup>a</sup>	--	--	21 (5.1) <sup>b</sup>
Leaves	61 (10.1) <sup>a</sup>	--	--	14 (4.6) <sup>b</sup>
Stems	30 (6.0) <sup>a</sup>	--	3 (0.4)	16 (2.6) <sup>b</sup>
31 (4.8) <sup>a</sup>	--	--	20 (1.5) <sup>b</sup>	13 (2.0) <sup>b</sup>
Herbs				
Leaves	63 (11.1) <sup>a</sup>	1 (0.5)	18 (1.5) <sup>b</sup>	36 (2.9) <sup>b</sup>
Stems	334 (34.8) <sup>a</sup>	209 (32.2)	36 (2.3) <sup>c</sup>	75 (2.5) <sup>a</sup>
VEGETATION TOTAL				62 (3.8) <sup>a</sup>
LITTER				228 (15.8) <sup>b</sup>
PINE				
Needles	1017 (70.2) <sup>a</sup>	99 (17.9)	172 (29.4) <sup>d</sup>	336 (14.8) <sup>c</sup>
Other	939 (59.7) <sup>a</sup>	--	111 (29.1)	468 (20.2) <sup>b</sup>
UNDERSTORY				
Shrub				
Forest floor	--	--	148 (28.5)	114 (15.6) <sup>a</sup>
Standing dead	--	--	60 (21.9)	115 (8.8) <sup>a</sup>
Herb	--	--	87 (6.7) <sup>b</sup>	61 (10.6) <sup>a</sup>
LITTER TOTAL	1252 (25.1) <sup>a</sup>	101 (18.9)	<1	265 (21.2) <sup>b</sup>
GRAND TOTAL	1585 (40.6) <sup>a</sup>	310 (44.3)	320 (39.0) <sup>d</sup>	79 (10.1) <sup>a</sup>
				10 (12.5) <sup>b</sup>
				54 (13.9) <sup>a</sup>
				52 (5.7) <sup>b</sup>
				460 (23.3) <sup>c</sup>
				636 (24.2) <sup>b</sup>
				701 (56.8) <sup>c</sup>
				864 (34.6) <sup>b</sup>

Table 36. Magnesium standing crops, site 2 wet season burn plot.

COMPARTMENT	MAGNESIUM (mg/m <sup>2</sup> )			
	PREBURN	POSTBURN	2 MONTH	7 MONTH
<b>VEGETATION</b>				
SHRUBS	744(12.9) <sup>a</sup>	656(243.5)	41(3.2) <sup>d</sup>	152(14.9) <sup>c</sup>
Palms	78(18.1) <sup>a</sup>	67(8.3)	30(3.2) <sup>b</sup>	339(42.4) <sup>b</sup>
<u>Sabal Palmetto</u>	67(19.7)	--	10(1.8)	70(11.6) <sup>a</sup>
<u>Serenoa repens</u>	11(3.3)	--	10(3.9)	--
Hardwoods	666(20.5) <sup>a</sup>	589(245.3)	12(3.6) <sup>d</sup>	95(15.9) <sup>c</sup>
Leaves	372(18.3)	254(110.2)	--	269(37.6) <sup>b</sup>
Stems	294(3.9)	338(135.4)	--	20(33.8) <sup>b</sup>
<u>Gouettardia Scabra</u>	140(10.2)	130(16.1)	<1	6(1.3)
Leaves	60(6.1)	49(9.5)	--	44(8.8) <sup>a</sup>
Stems	80(6.4)	81(7.8)	--	31(6.1) <sup>a</sup>
HERBS	44(11.5) <sup>a</sup>	1(1.1)	11(2.0) <sup>b</sup>	31(2.6) <sup>a</sup>
VEGETATION TOTAL	788(22.8) <sup>a</sup>	657(244.6)	53(2.0) <sup>d</sup>	50(4.7) <sup>a</sup>
LITTER				389(44.1) <sup>b</sup>
PINE	991(36.8) <sup>a</sup>	374(71.0)	292(25.1) <sup>b</sup>	314(33.7) <sup>b</sup>
Needles	917(28.2)	--	--	217(15.3)
Other	74(21.0)	--	--	98(19.5)
UNDERSTORY	465(62.0) <sup>a</sup>	67(49.2)	419(140.3) <sup>a</sup>	392(139.9) <sup>a</sup>
Shrub	--	--	419(140.3)	392(139.9)
Forest floor	--	--	114(27.4)	157(20.7)
Standing dead	--	--	306(115.6)	235(23.3)
Herb	--	--	<1	<1
LITTER TOTAL	1457(30.7) <sup>a</sup>	440(114.8)	711(141.1) <sup>b</sup>	707(54.7) <sup>b</sup>
GRAND TOTAL	2244(48.0) <sup>a</sup>	1098(158.7)	764(142.0) <sup>b</sup>	890(40.9) <sup>b</sup>
				941(63.7) <sup>b</sup>

Table 37. Magnesium standing crops, site 2 dry season burn plot.

VEGETATION	MAGNESIUM (mg/m <sup>2</sup> )			
	PREBURN	POSTBURN	2 MONTH	8 MONTH
<b>CORPUSPANT</b>				
SUBRUBS	677(138.4) <sup>a</sup>	486(95.1)	23(1.5) <sup>c</sup>	262(10.4) <sup>b</sup>
<i>Sabal palmietto</i>	84(23.1) <sup>a</sup> 60(113.3)	13(5.5) --	18(2.1) <sup>b</sup> 16(1.9) 21(1.6)	66(12.2) <sup>a</sup> -- --
<i>Serenoa repens</i>	24(11.5)	--	4(0.5) <sup>c</sup>	94(24.4) <sup>a</sup> --
HARDWOODS	593(134.1) <sup>a</sup>	472(94.6)	196(20.1) <sup>b</sup>	163(17.2) <sup>b</sup>
Leaves	247(64.3)	131(32.2)	--	104(13.5)
Stems	346(70.0)	342(69.2)	--	59(15.3)
GUETTARDA scabra	165(37.3)	87(8.9)	25(3.9)	40(9.2)
Leaves	63(15.9)	16(3.1)	--	21(4.9)
Stems	102(22.0)	71(5.4)	--	18(4.4)
HERBS	60(16.8) <sup>a</sup>	<1	5(0.6) <sup>c</sup>	40(7.9) <sup>ab</sup>
VEGETATION TOTAL	737(126.7) <sup>a</sup>	486(95.1)	28(1.6) <sup>c</sup>	27(1.9) <sup>b</sup>
LITTER			303(14.4) <sup>b</sup>	283(34.1) <sup>b</sup>
PINE	1438(122.5) <sup>a</sup>	28(7.7)	161(14.8) <sup>c</sup>	318(18.3) <sup>b</sup>
Needles	1343(115.2)	--	141(9.4)	380(20.3) <sup>b</sup>
Other	96(10.9)	--	21(6.0)	272(17.1)
UNDERSTORY	331(78.0) ab	12(7.9)	548(151.9) <sup>a</sup>	46(15.3)
Shrub	--	--	548(151.9)	215(24.6) <sup>b</sup>
Forest floor	--	--	159(45.0)	205(29.1)
Standing dead	--	--	389(126.3)	331(22.8)
Herb	--	--	<1	49(21.1)
LITTER TOTAL	1769(150.5) <sup>a</sup>	40(15.4)	709(144.1) <sup>b</sup>	6(3.1)
GRAND TOTAL	2506(195.6) <sup>a</sup>	526(104.9)	737(141.3) <sup>b</sup>	10(5.2)
			587(36.4) <sup>b</sup>	595(41.8) <sup>b</sup>
			889(127.4) <sup>b</sup>	879(165.0) <sup>b</sup>

#### BIOGRAPHICAL SKETCH

James R. Snyder received a B.S. in biology from Ursinus College in Collegeville, Pennsylvania, and an M.A. in botany from the University of North Carolina, Chapel Hill. After teaching botany for a year at Moravian College in Bethlehem, Pennsylvania, he entered the University of Florida. In May 1984 he begins employment as research biologist at Big Cypress National Preserve. He and wife Jean are the proud parents of two daughters.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of  
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